

Mandibular Postcanine Dentition From the Shungura Formation, Ethiopia: Crown Morphology, Taxonomic Allocations, and Plio-Pleistocene Hominid Evolution

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ABSTRACT Over 200 hominid specimens were recovered by the International Omo Expedition of 1967–1976. Despite the fragmentary nature of this primarily dental collection, these hominid remains represent a major body of evidence about hominid evolution in eastern Africa during the 2–3 myr time period. Our analysis of the Omo dental collection is based on a large comparative sample of 375 quantifiable mandibular postcanine teeth of *A. afarensis*, *A. africanus*, *A. aethiopicus*, *A. boisei*, *A. robustus*, and early *Homo*. A total of 48 isolated mandibular premolars and molars of the Omo collection spanning the 2–3 myr time period is sufficiently preserved to allow reliable serial allocations and intertaxon comparisons and is the object of study in this paper. We present taxonomic identifications of these teeth and seven other mandibular specimens preserving tooth crowns. Metric analyses of this study include cusp area and crown shape variables taken on occlusal view diagrams. Nonmetric analyses were based on simultaneous observations of all relevant material to ensure accuracy of categorical evaluations. First, a combined metric and morphological evaluation was conducted to allocate each Omo tooth to either robust or nonrobust categories. Further taxonomic affinities were then examined. Our results indicate that nonrobust and robust lineages cooccur by circa 2.7 myr. We consider the Shungura robust specimens from Members C through F to represent *A. aethiopicus*. A significant phenetic transformation occurs at circa 2.3 myr, with the mosaic emergence of the derived *A. boisei* morphology across Member G times. Characterization of the East African nonrobust lineage is more difficult because of the comparatively subtle morphological differences seen among the dentitions of *A. afarensis*, *A. africanus*, and early *Homo*. The earlier Members B and C nonrobust specimens are difficult to evaluate and are considered indeterminate to genus or species. Both molars and premolars from Members E through G exhibit phenetic similarities to the early *Homo* condition and are considered as aff. *Homo* sp. indet. At present, there is no indication of multiple species in the Omo nonrobust sample at any time horizon. The 2–2.4 myr Omo nonrobust specimens exhibit some similarities to the stated *Homo* “*rudolfensis*” condition in size and morphology and are likely to represent the ancestral condition of

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the genus *Homo*. The bearing of these results on interpretations of early hominid evolution and diversification is considered. © 1996 Wiley-Liss, Inc.

The International Omo Expedition commenced in 1967 and continued through 1976. The American contingent of this expedition, directed by one of us (F.C.H.), worked annually in the field until 1974. Research in the lower Omo valley focused on the deposits and their fossil contents and was instrumental in establishing a chronostratigraphic framework for the Plio-Pleistocene of eastern Africa. Hominid remains were recovered during the first field season (Arambourg and Coppens, 1967, 1968; Howell, 1968) and annually thereafter, totalling 217 specimens (Howell, 1969a,b; Howell and Coppens, 1973, 1974, 1976; Howell and Wood, 1974; Boaz and Howell, 1977; Rak and Howell, 1978; Coppens, 1970, 1971, 1973a,b, 1980; Coppens and Sakka, 1983; Deloison, 1986). These range from the lower to the uppermost levels in stratigraphic distribution, with most of the sample coming from deposits of circa 3.2 to 2.2 myr.

The East Rudolf Research Expedition, running from 1968–1976, first advanced interpretations that the major fossiliferous deposits and abundant hominid remains of the Koobi Fora Formation spanned a comparable time depth, with the KBS tuff estimated at circa 2.4 or 2.6 myr (for a historical overview see Brown, 1994). However, subsequent geological work in the 1980s established a major depositional hiatus from circa 2.5 to 2.0 myr. This resulted in a lack of hominids deriving from the 3 to 2 myr time interval (Feibel et al., 1989), with the exception of the KNM-ER 5431 mandibular postcanine dental set dated to circa 2.7 myr. In the 1980s, further research at Lake Turkana established a more continuous fossiliferous sequence on the west side of the lake. These deposits yielded a cranium and mandible at circa 2.5 myr variously attributed to *A. aethiopicus* (e.g., Howell et al., 1987; Kimbel et al., 1988) or an early segment of the *A. boisei* lineage (Walker et al., 1986; Leakey and Walker, 1988). Other East African hominid specimens from the 2–3 myr time range have not been reported, until the Chemeron tem-

poral was redated to circa 2.4 myr accompanied by a reevaluation of its taxonomic status as an early example of the genus *Homo* (Hill et al., 1992; but see Feibel, 1992; Tobias, 1993). Work near Lake Malawi yielded a *Homo* mandible estimated to be circa 2.3–2.5 myr old (Schrenk et al., 1993; Bromage et al., 1995).

Despite these new finds and analyses, the Omo hominid collection remains numerically the largest body of evidence about hominid evolution in eastern Africa from the 2–3 myr time range. Its importance lies in the abundance and precise chronological placement of the hominid remains, but their fragmentary nature renders interpretations difficult. A total of 193 isolated teeth forms the bulk of the Omo hominid sample. Interpretations of these teeth have been based on broad but general morphological comparisons (Howell and Coppens, 1976; Howell, 1978; Howell et al., 1987; Coppens, 1980), which were presented as tentative assessments. Because mandibular and cranial remains with associated dentitions were few and dispersed widely through time, in practice, no reference sample exists from which specific morphological criteria for the positional and taxonomic allocations of isolated teeth can be built. Without unequivocal and unambiguous guidelines for the initial positional/taxonomic sorting of the isolated teeth, interpretations have been plagued by an unknown degree of inherent uncertainty. For example, in our view, some more recent studies incorporating the Omo collection as an object of renewed examination (Hunt and Vitzthum, 1986; Ramirez-Rozzi, 1993) have reached invalid and/or unsupported conclusions.

A more systematic treatment of the Omo dental sample was undertaken with the specific aim of extracting maximal information from the fragmentary and isolated nature of the vast majority of specimens. In the present paper, we focus on the mandibular postcanine dentition which is both more taxonomically diagnostic within Plio-Pleistocene

hominids (Wood and Engleman, 1988; Suwa, 1990) and most abundantly represented in the Omo collection.

Our analysis of the Omo dentition is based on comparisons with a large body of early hominid dental material from South and East Africa. In particular, we have assembled sufficiently accurate high quality casts of tooth crowns comprising 330 quantifiable mandibular postcanine teeth (not counting antimeres) of *A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei*, and a mixed sample of early *Homo*. More fragmentary remains form additional portions of this cast collection, while another 45 measurable specimens from Sterkfontein were included in the comparative sample using photographs. This enabled accurate cross-taxon and cross-position comparisons based on simultaneous observations of all relevant specimens. In evaluating specific morphological features, seriation of specimens by degree of expression of the particular feature under consideration was undertaken using the cast collection. In this way, not only could precise guidelines for the initial positional sorting of the Omo teeth be made, but evaluations of detailed crown morphology could be undertaken with minimum observational error.

We start our analysis by formulating explicit and presumably more reliable positional allocations of each Omo tooth (see below). Taxonomic affinities are then evaluated. This latter task is rendered difficult because a priori expectations regarding taxa represented in the Omo succession are not available, aside from very general ones. From cranial and mandibular remains, a robust *Australopithecus* lineage has been suggested to have existed in the Lake Turkana basin from uppermost Member C to lower Member G times (Howell, 1969a; Coppens, 1970; Rak and Howell, 1978; Coppens and Sakka, 1983; Leakey and Walker, 1988). A large portion of the isolated dentition has also been allocated to *A. boisei*, although different workers have suggested varying first occurrences of this taxon (e.g., Howell and Coppens, 1976; Grine, 1985; Ramirez-Rozzi, 1993). Presence of early *Homo* has been clearly documented from upper Member G (Boaz and Howell, 1977) but less certainly

from other levels. However, largely from the isolated teeth, a nonrobust taxon has been considered to occur continuously throughout the Shungura Formation.

In the present study, we follow the working hypothesis that single robust and nonrobust lineages cooccur in eastern Africa subsequent to the first appearance of the former. No other assumptions are made regarding the timing of robust *Australopithecus* emergence, the characteristics of each lineage, or any evolutionary change through time. We also take the stance that the two well-documented robust *Australopithecus* taxa, *A. robustus* and *A. boisei*, share many derived morphological features, although not all such similarities may actually indicate common descent. Regardless of homology or parallelism in *A. robustus/boisei* similarities, we point out that it is logical to attribute any isolated specimen to an unspecified robust taxon, if it shares the derived features under consideration. Conversely, specimens that do not exhibit the robust features can operationally be allocated to the nonrobust lineage.

In the present study, initial taxonomic evaluations of the Omo dentition were made along the above lines. Further comparisons follow, in which more specific patterns are investigated. When do the uniquely derived features of *A. boisei* appear? How does the earlier segment of the East African robust lineage compare with *A. robustus*? How long does an *A. afarensis* morphology persist through time? Is *A. africanus* represented at Omo? When does a more *Homo* as opposed to an *A. africanus*- or *A. afarensis*-like morphology appear? The purpose of this study is to present unambiguously information regarding the above questions, based solely on the dental evidence. Such conclusions are meant to stand on their own and can be integrated with other existing or forthcoming craniomandibular evidence.

MATERIALS AND METHODS

Materials

The comparative sample of the present study consists of mandibular premolars and molars attributed to *A. afarensis*, *A. africanus*, *A. robustus*, *A. boisei*, and early *Homo*

TABLE 1. Mandibular postcanine sample of the present study

	P3	P4	M1	M2	M3	Total
<i>A. afarensis</i>	18	13	14	18	11	74
<i>A. africanus</i>	10	13	20	26	22	91
<i>A. robustus</i>	17	18	23	20	22	100
<i>A. boisei</i>	7	10	9	11	10	47
Early <i>Homo</i>	11	8	15	13	16	63
Total	63	62	81	88	81	375
Omo	13	12	10	12	18	65
Shungura						

available to the authors for study as of summer 1986 and 1988 for the South and East African collections, respectively. These are summarized in Table 1.

The *A. afarensis* sample includes specimens from the Hadar Formation and Upper Laetolil Beds, the *A. robustus* sample those from Kromdraai and Swartkrans Members 1 and 2, and the *A. boisei* sample those from the KBS and Okote Members of the Koobi Fora Formation, Beds I and II Olduvai Gorge, and the Humbu Formation at Lake Natron. The *A. africanus* sample includes specimens from Taung, Makapansgat, and Sterkfontein Member 4 as well as those from Sterkfontein with a Member 4/5 provenience. We are presently not persuaded that there is sufficient evidence to allocate any of the Sterkfontein specimens to other taxa, such as *A. robustus* or *Homo*, despite suggestions to the contrary (Clarke, 1988; Conroy and Vannier, 1991; Kimbel and Rak, 1993). Wood (1991a) has shown that metric variation of the *A. africanus* sample is not excessive when compared to that of the well-defined *A. boisei* hypodigm. The early *Homo* sample is taxonomically heterogeneous and includes specimens attributable to two or three species of *Homo* from the upper Burgi, KBS and Okote Members of the Koobi Fora Formation, Beds I and lower/middle Bed II at Olduvai, Sterkfontein Member 5, and Swartkrans Members 1 and 2. Some of these specimens undoubtedly represent early *Homo erectus* (or *H. ergaster*), while others are referable to *Homo habilis/rudolfensis*. Although some of these specimens have been allocated to species (e.g., Wood, 1991b), we did not break down the early *Homo* sample in this study because further analyses are needed for a more complete sorting of all

specimens included in the "early *Homo*" sample of the present study.

Table 2 lists the mandibular premolars and molars from the Shungura Formation considered in the present study. These represent the better preserved dentitions on which more reliable serial and taxonomic evaluations can be made and consist of 48 isolated teeth (9 P3s, 5 P4s, 9 M1s, 9 M2s, 16 M3s) spanning the 3 to 2 myr time range of the Shungura Formation. A further seven mandibular specimens with partial dentitions from the same stratigraphic interval are included in this analysis, as are mandibular specimen KNM-WT16005 from the Nachukui Formation and dental set KNM-ER5431 from the Koobi Fora Formation. These two Kenyan specimens are dated to circa 2.5 myr and 2.7 myr, respectively (Feibel et al., 1989).

We consider the serial and gnathic allocations of these isolated teeth to be secure, while we differ in interpretations regarding some of the more fragmentary pieces not included in the present study. Serial morphological differences were comparatively more clear on the heteromorphic premolars than on the molars. Thus, reasons for allocations have been outlined only when deemed necessary for the premolars (Suwa, 1990), while a more systematic account has been presented for the molars (Suwa, in press). This latter study demonstrated the reliability of a method combining morphological and morphometric criteria in differentiating M1 and M2s, emphasizing the need of incorporating the unrestricted approach of classification (sensu Albrecht, 1992) when applying discriminant function analysis (Suwa, in press). All first and second molars included in the present study were comprehensively evaluated in that study, with the exception of one relatively complete but worn molar (L824-5 M1) serially allocated simply from application of the morphological criteria.

Methods

A combined metric and morphological evaluation detailed below was conducted to allocate each Omo specimen to either robust or nonrobust categories, and to evaluate further taxonomic affinities thereafter. These variables are listed in Table 3. A full descrip-

TABLE 2. *Omo specimens evaluated in the present study*¹

	Specimen	Member	Taxonomic designation
Isolated P3	OMO18-31	C	<i>A. aethiopicus</i>
	OMO18-33	C	<i>Australopithecus/Homo</i> gen. and sp. indet.
	OMO177-4525	E	aff. <i>Homo</i> sp. indet.
	OMO33-5496	F	aff. <i>Homo</i> sp. indet.
	OMO123-5495	F	aff. <i>Homo</i> sp. indet.
	L398-120	F	<i>A. aethiopicus</i>
	L465-111	F	<i>A. aethiopicus</i>
	OMO29-43	G	aff. <i>Homo</i> sp. indet.
	OMO75i-1255	G	aff. <i>Homo</i> sp. indet.
Isolated P4	L51-79	C	<i>A. aethiopicus</i>
	L51-80	C	<i>Australopithecus/Homo</i> gen. and sp. indet.
	L338x-40	E	<i>A. aethiopicus</i>
	OMO33-508	F	<i>A. aethiopicus</i>
	L628-4	G	<i>A. aff. aethiopicus/boisei</i>
Isolated M1	OMO212-1950	B	<i>Australopithecus/Homo</i> gen. and sp. indet.
	OMO18-34	C	<i>A. aethiopicus</i>
	L45-2	C	<i>Australopithecus/Homo</i> gen. and sp. indet.
	L51-1	C	<i>Australopithecus/Homo</i> gen. and sp. indet.
	L824-5	D	<i>Australopithecus/Homo</i> gen. and sp. indet.
	L26-1g	E	aff. <i>Homo</i> sp. indet.
	OMO75s-15	G	aff. <i>Homo</i> sp. indet.
	OMO195-1630	G	aff. <i>Homo</i> sp. indet.
	L628-9	G	<i>A. aff. boisei</i>
Isolated M2	L795-1	B/C	Indeterminate
	L62-17	C	<i>A. aethiopicus</i>
	F22-1a	F	<i>A. aethiopicus</i>
	L157-35	F	<i>A. aethiopicus</i>
	OMO47-46	G	<i>A. aff. boisei</i>
	OMO47-1500	G	<i>A. aff. boisei</i>
	OMO136-2	G	<i>A. aff. boisei</i>
	L7-279	G	aff. <i>Homo</i> sp. indet.
	L628-10	G	aff. <i>Homo</i> sp. indet.
Isolated M3	OMO28-30	B	Indeterminate
	L1-294	B	<i>Australopithecus/Homo</i> gen. and sp. indet.
	L1-398	B	<i>Australopithecus/Homo</i> gen. and sp. indet.
	L2-89	B	<i>Australopithecus/Homo</i> gen. and sp. indet.
	L9-11	D	<i>Australopithecus/Homo</i> gen. and sp. indet.
	L296-1	D	<i>A. aethiopicus</i>
	L338x-39	E	<i>A. aethiopicus</i>
	OMO33-9	F	<i>A. aethiopicus</i>
	OMO33-6172	F	<i>A. aethiopicus</i>
	F22-1b	F	<i>A. aethiopicus</i>
	L28-30	F	aff. <i>Homo</i> sp. indet.
	L398-630	F	<i>A. aethiopicus</i>
	OMO75s-16	G	aff. <i>Homo</i> sp. indet.
	OMO136-1	G	<i>A. aff. boisei</i>
	L628-2	G	<i>A. aff. boisei</i>
	L628-3	G	<i>A. aff. boisei</i>
	L55-33	C	<i>A. aethiopicus</i> (P4)
Mandibles	OMO57.4-41	E	<i>A. aethiopicus</i> (partial P4)
	L860-2	F	<i>A. aethiopicus</i> (P3, P4, M2)
	OMO75-14	G	aff. <i>Homo</i> sp. indet. (P3 through M3)
	L7a-125	G	<i>A. aff. boisei</i> (I2 through M3)
	L74a-21	G	<i>A. aff. boisei</i> (C, P4)
	L427-7	G	<i>A. aff. boisei</i> (P3, P4, M2)

¹Tooth crowns preserved in the partial mandibles are listed in parentheses. The above listed isolated teeth and mandibles are figured in the Appendix or in Coppens (1970, 1971, 1973a,b), Howell (1969a), or Howell and Coppens (1976).

tion of these is available in Suwa (1988, 1990, in press) and Suwa et al. (1994) and is not repeated here.

Statistical analyses used include univariate and multivariate methods for both metric and categorical variables. Univariate analysis of the continuous variables include

one-way ANOVA tests on taxon means, while principal components and canonical variate analyses of the raw scaled metric variables were employed to summarize major across-taxon trends or to contrast taxonomic groups. Because the *Omo* specimens need not belong to any of the five taxonomic

TABLE 3. Metric and categorical variables relevant to the present study¹

Item	Tooth position	Abbreviated description
AREA	P3-M3	Measured occlusal view crown area
PDPCT	P3-M3	Measured protoconid area divided by AREA
MDPCT	P3-M3	Measured metaconid area divided by AREA
HDPCT	M1-M3	Measured hypoconid area divided by AREA
HLDPCT	M1-M3	Measured hypoconulid area divided by AREA
EDPCT	M1-M3	Measured entoconid area divided by AREA
C6PCT	M1-M3	Measured cusp 6 area divided by AREA
POSTPCT	P3, P4	Measured talonid area divided by AREA
BLTINDX	P3, P4	Mesiodistal length divided by buccal crown length
BRINDX	P3, P4	Trigonid breadth divided by talonid breadth
LTBRNDXE	P3	Square root of AREA divided by oblique crown breadth
MDANG	P3, P4	Angle between buccal crests and line connecting pd and md
OBLQANG	P3	Angle between buccal crests and oblique crown axis
LONGANG	P3, P4	Angle between buccal crests and longitudinal groove
BASBUCAS	P3, P4	Basal buccal crown asymmetry
MLINGCNT	P3	Mesiolingual crown contour
DLINGCNT	P3	Distolingual crown contour
EDJMBUCP	P3	Configuration of mesiobuccal enamel line
MMRHT	P3	Height of buccal segment of mesial marginal ridge
MMRLNG	P3	Development of lingual segment of mesial marginal ridge
TRCRST	P3, P4	Transverse crest prominence
MDPOS	P3, P4	Mesiodistal position of metaconid
MDINDIV	P3	Metaconid prominence relative to adjacent crown structures
BUCWALS	P3, P4	Slope of buccal crown face
MESBUCGR	P3, P4	Development of mesial buccal groove
DISBUCGR	P3, P4	Development of distal buccal groove
DLINGCSP	P3, P4	Development of distolingual cusplet
TOTLTSC	M1-M3	Mesiodistal length divided by square root of AREA
ANTBRSC	M1-M3	Anterior crown breadth divided by square root of AREA
MINBRSC	M1-M3	Minimum midcrown breadth divided by square root of AREA
MAXBRSC	M1-M3	Maximum midcrown breadth divided by square root of AREA
POSTBRSC	M1-M3	Posterior crown breadth divided by square root of AREA
DISTBRSC	M1-M3	Relative crown breadth at position of hd/hld junction
DPRJLTSC	M1-M3	Relative crown length distal to hd/hld junction

¹ See Suwa (1988, 1990), Suwa et al. (1994), and Suwa (in press) for precise definitions of these variables.

groups of the comparative sample, posterior probabilities of membership were not calculated for any specimen. Rather, these multivariate analyses are meant to summarize ranges of phenetic variation occurring in the known samples so that the morphological affinities of the Omo specimens can be evaluated. Similarly, Kruskal-Wallis tests were conducted on the categorical variables to test for equivalence among taxa, and multidimensional scaling analysis was used to summarize these trends. In the latter analysis, Kruskal's monotonic transformation method was used in reducing the data structure into two dimensions.

SORTING TO ROBUST AND NONROBUST CATEGORIES

Mandibular premolars

Analysis of the Omo mandibular premolars have, for the most part, been presented

elsewhere in detail (Suwa, 1988, 1990). Only some summarizing points will be made here, accompanied by new results of multidimensional scaling analysis. Both *A. robustus* and *A. boisei* share a distinctive mandibular P3 morphology (Fig. 1), consisting of an increased occlusal area, a shift of metaconid position relative to the protoconid crests, increased talonid area at the expense of the mesiobuccal crown, reduced asymmetry of the crown, and reduced topography of the occlusal surface (Suwa, 1988, 1990). Relative cusp proportions of the robust *Australopithecus* P3 cannot be attained by extrapolation of allometric relationships observed within the nonrobust samples, and are best considered a derived condition beyond simple increase in crown size (Wood and Uytterschaut, 1987; Suwa, 1990). This structural package can be interpreted as an adaptation for increased crushing/grinding

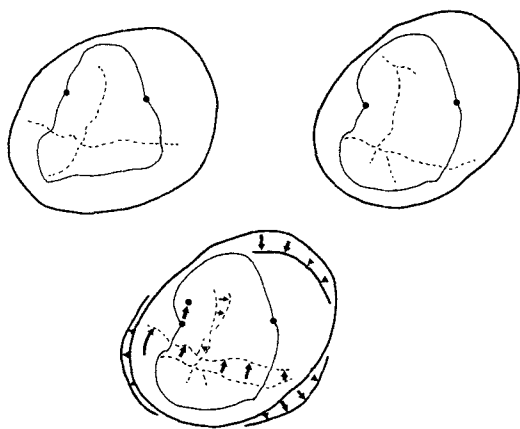


Fig. 1. Schematic comparison of robust and nonrobust mandibular P3s. **Top left:** SK857, *A. robustus*. **Top right:** STS51, *A. africanus*. **Bottom:** The two superimposed by approximate matching of the mesial and distal protoconid crests, both specimens scaled to equivalent crown area. Right crowns, mesial to the top. Note the large talonid, small protoconid, and mesially placed metaconid in the robust P3.

surface available from the initial stages of wear. Suwa (1990) suggested that the relative cusp position of the robust *Australopithecus* mandibular P3 probably reflects occlusal relationships imposed by the distinct maxillary dental arcade with a canine position lingual to the maxillary P3 (e.g., Robinson, 1956; Wallace, 1978).

Three relative cusp areas and two indices measuring aspects of talonid expansion segregate the robust and nonrobust samples as summarized in Figure 2 by principal components analysis. Eight nonmetric variables show a complete separation with no overlap in range of variation between the robust and nonrobust taxa as expressed by multidimensional scaling of the categorical data (Fig. 3). One *A. robustus* specimen, SK96, fails to group with the other robust specimens in the metric expression but does so with the nonmetric features.

Turning to the mandibular P3s of the Shungura Formation, three isolated P3s (OMO18-31, L398-120, L465-111) and those belonging to partial mandibles L860-2 and L427-7 are demonstrated to exhibit robust australopithecine affinities (Fig. 2,3). The P3 of the L7a-125 mandible is too worn and damaged to be included in these quantitative

analyses but also exhibits the robust morphological pattern. Six isolated P3s (OMO18-33, OMO177-4525, OMO33-5496, OMO123-5495, OMO29-43, OMO75i-1255) conversely group with the nonrobust specimens, as does the OMO75-14a P3. The ER5431 P3 exhibits the nonrobust pattern, while WT16005 aligns with the robusts.

With the mandibular P4s, a clear robust vs. nonrobust morphological dichotomy does not occur, with large overlap in range of variation between *A. robustus* and the three nonrobust taxa in the measured features of the crown (Wood and Uytterschaut, 1987; Suwa, 1988). However, some nonmetric morphological features do show strong trends, enabling the Omo P4s to be assessed. These features relate to increased area and reduced topography of the occlusal surface, talonid development, and reduced crown asymmetry in the robust taxa, paralleling the P3 condition in part but at more subtle manifestations. Multidimensional scaling plots of these four categorical variables enable evaluation of the Shungura P4s (Fig. 4). Specimens with both P3 and P4 exhibit concordant results in analyses of both premolar positions. The isolated Member C P4s, L51-79 and L51-80, are suggested as likely representatives of robust and nonrobust taxa, respectively. The Member F P4, OMO33-508, fell within the robust and at the very end of the known nonrobust range of variation. Together with other features such as flat occlusal wear and large talonid size, this specimen is interpreted to represent a robust *Australopithecus* taxon.

Mandibular molars

Metric and nonmetric variation of the mandibular molars less clearly separate robust and nonrobust taxa. Thus, for the molars, a combined criteria approach was taken. Features or feature complexes exhibiting sufficient trends but with substantial overlap in ranges of robust and nonrobust variation include absolute crown size, cusp area proportions, crown shape as expressed by linear measurements, presence/absence and size of accessory cusps C6 and C7, wear pattern, and enamel thickness.

Tooth size was gauged by measured crown area, cusp proportions by relative cusp ar-

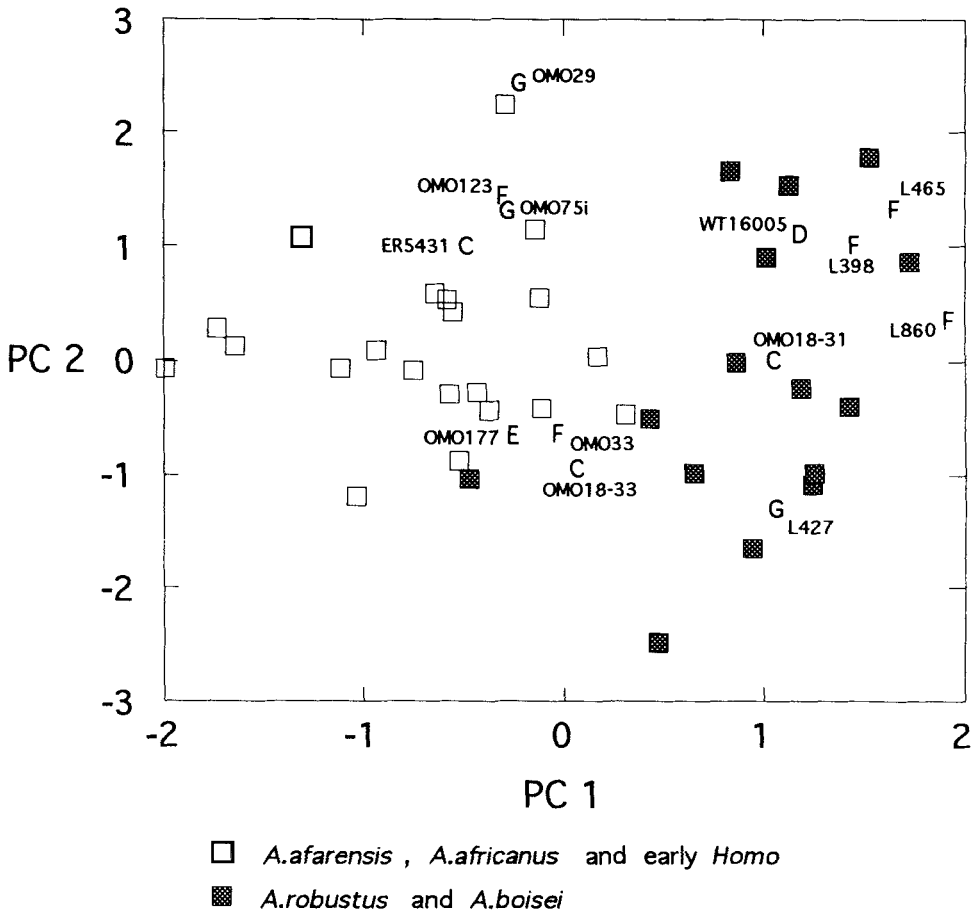


Fig. 2. Principal components analysis of five metric variables of the mandibular P3. Input variables (see Table 3) are PDPCT, MDPCT, POSTPCT, BLTINDX, BRINDX. Raw scaled variables were used without logarithmic transformations. Only specimens with all five variables measured or estimated were included in the

analysis. A large positive score in the first principal component indicates a large and broad talonid, small protoconid, and large midcrown length. See Suwa (1990) for further details. Letters indicate plot position and stratigraphic level of each Omo specimen.

eas, and crown shape by the seven scaled linear variables (Fig. 5). The latter two sets of metrics were summarized by canonical variate analysis of the raw scaled variables, with the first axis representing the major intertaxon trends. An examination of the canonical variates suggest that the first axis can be taken to reflect robust vs. nonrobust contrasts, the robust molars being characterized by relatively larger and posteriorly extended distal cusps. Affinities of the Omo specimens were determined conservatively. Only when a specimen fell within the known range of variation of either robust or nonro-

bust samples but outside that of the other was it interpreted to exhibit robust or nonrobust affinities. Exact applications of this approach were conducted on measured crown area and in the first axis scores of the canonical variate analyses of relative cusp areas and scaled linear variables expressing crown shape.

Known occurrences of C6 and C7 in M1 and M2s (Wood and Abbott, 1983; Suwa et al., 1994) suggest that lack of C6 and presence of C7 are highly suggestive of a nonrobust taxon. In particular, presence or absence of the C6 sorts the comparative sample

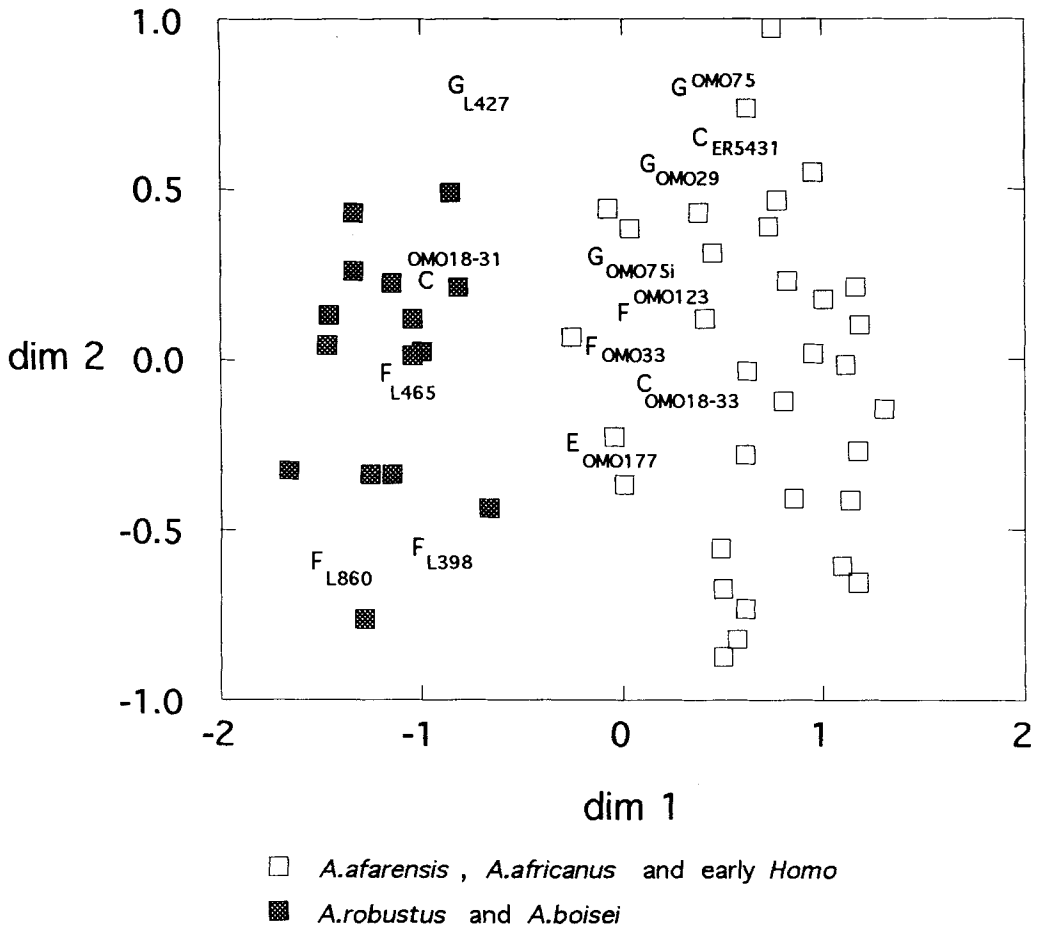


Fig. 3. Multidimensional scaling of eight nonmetric variables of the mandibular P3. Input variables (see Table 3) are MMRHT, MMRLING, TRCRST, MDPOS, DLINGCSP, BASBUCAS, BUCWALS, MESBUCGR. Specimens with five or more variables scored were included in the analysis. The first axis segregating robust from nonrobust P3s relates to all eight variables, with Kendall's coefficients of rank correlation greater than

0.7 and 0.5 with the first and latter four variables, respectively. This indicates a tendency for robust *Australopithecus* P3s to exhibit a high mesial marginal ridge, a low trigonid crest, a mesial metaconid position, a developed distolingual cusplet, weak basal buccal asymmetry, a relatively vertical buccal crown face, and a weak mesial buccal groove. Letters indicate plot position and stratigraphic level of each Omo specimen.

correctly in over 80% of the M1s. A C6 larger than a certain size is also highly indicative of a robust affinity, while a small or absent C6 in the M2 would suggest the opposite. In the M3, C6 relative to hypoconulid size forms a guideline for differentiating robust and nonrobust specimens. Approximately 85% of the entire comparative sample can correctly be allocated to robust and nonrobust categories by using a C6 to hypoconulid area ratio of 0.8 or 0.9 as cutoff points.

Enamel thickness was measured at natural fracture surfaces when it was possible to estimate lateral radial thickness. Despite differential enamel thickness by location within crown, along serial position, and between individuals of a taxon (Grine and Martin, 1988; Macho and Berner, 1993), measured thickness at natural breaks can be used to evaluate robust and nonrobust affinities if broad ranges are allowed. Taking results of Beynon and Wood (1986) and Grine

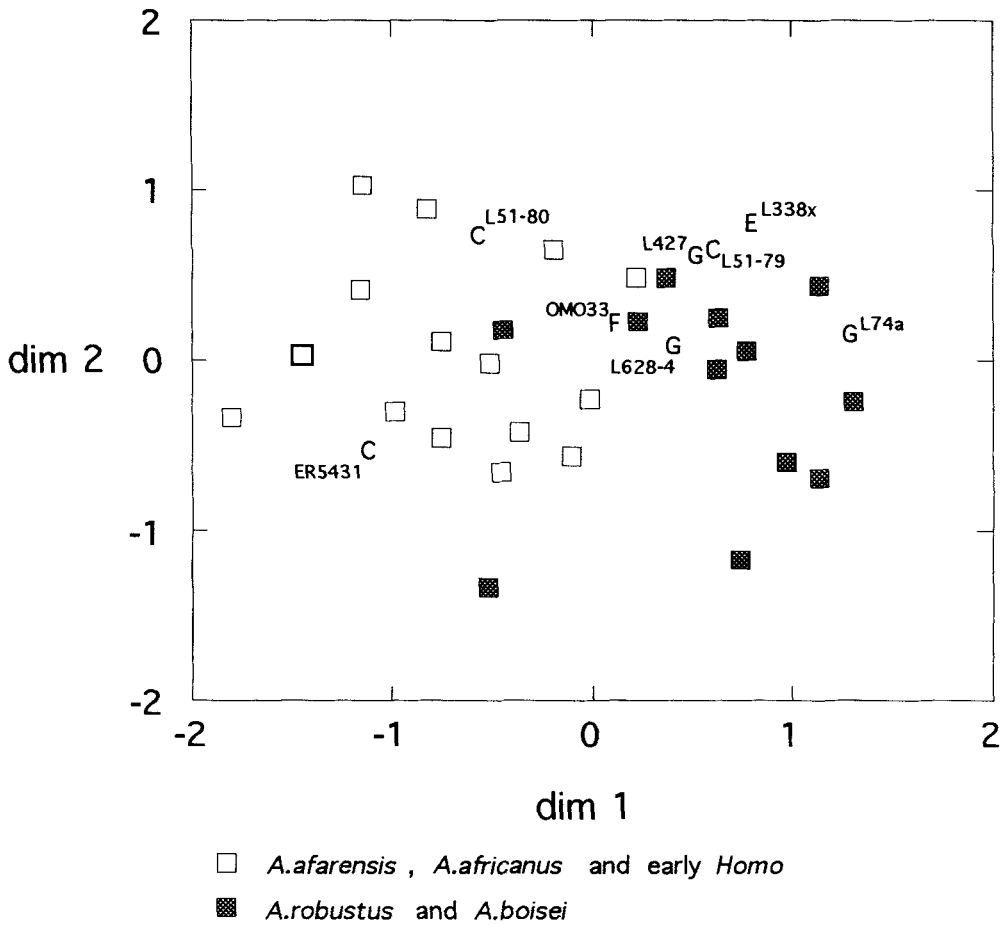


Fig. 4. Multidimensional scaling of four nonmetric variables of the mandibular P4. Input variables (see Table 3) are BASBUCAS, BUCWALS, TRCRST, DLINGCSP. Only specimens with all four variables scored were included in the analysis. The first axis tends to segregate robust from nonrobust P4s and relates to all four variables with Kendall's coefficients of rank cor-

relation ranging from 0.4–0.7. This indicates a tendency for robust *Australopithecus* P4s to exhibit a weak trigonid crest, a relatively vertical buccal crown face, weak basal buccal asymmetry, and a developed distolingual cusplet. Letters indicate plot position and stratigraphic level of each Omo specimen.

and Martin (1988) into account, lateral enamel thickness at lingual, mesial, or distal crown faces of 2.4 mm or greater was considered to indicate robust *Australopithecus* affinities. Wear pattern was evaluated in relation to degree of lingual cusp flattening and evaluated by direct comparisons with our comparative cast collection.

Table 4 summarizes the results of these evaluations. Most specimens can be allocated to robust or nonrobust categories without difficulty. Some comments follow on the

less obvious attributions. The L51-1 M1 is shown in Table 4 to exhibit a rather unclear situation, with the cusp 6 data pointing to a robust affinity and only the crown shape results strongly suggesting a nonrobust attribution. However, its C6 is approximately equivalent in size to the largest conditions known in nonrobust M1s (e.g., A.L. 266-1), while in measured crown area and cusp proportions it conforms to the nonrobust condition but is not tabulated as such because it falls within the end of the robust range.

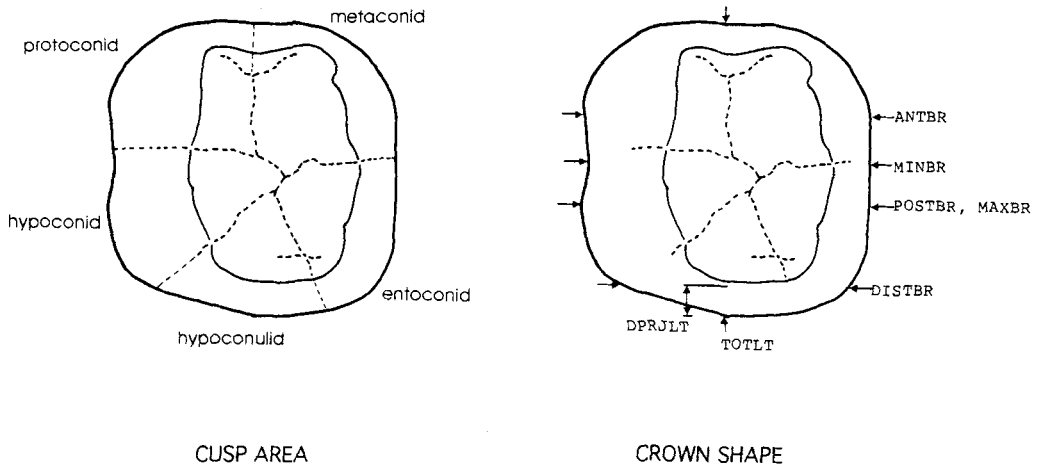


Fig. 5. Metric variables used in the analysis of mandibular molars. **Left:** Definition of the five major cusp areas. Relative cusp areas were obtained by dividing each cusp area with crown area. See Suwa et al. (1994) for further details. **Right:** Definition of the seven linear variables expressing occlusal view crown shape. TOTLT is length along the mesiodistal axis. ANTBR is maximum breadth at a position at or more mesial than midpoint of the mesial longitudinal groove. POSTBR is maximum breadth at a position at or more distal than the mesial end of the distal longitudinal groove. MAXBR is

maximum breadth at a position in between ANTBR and POSTBR levels. MINBR is the minimum breadth at a position in between the mesiobuccal and lingual grooves. DISTBR is breadth taken at the level of the hypoconid/hypoconulid boundary and crown margin junction. DPRJLT measures distal crown projection and is defined as the length of the crown along the mesiodistal axis distal to the DISTBR level. See Suwa (in press) for further details. In this analysis, all variables were scaled by the square root of crown area and are listed in Table 3 with a suffix of SC.

Thus, the overall affinities of L51-1 are clearly with the nonrobust category. The L26-1g M1 exhibits cusp proportions more as in robusts but crown shape and accessory cusps as in nonrobusts. We interpret the weight of the evidence to favor a nonrobust attribution.

The L795-1 M2 derives from low in the Shungura Formation with a B12/C1 provenience. It exhibits a nonrobust morphology but is extraordinarily large (measured crown area of 235 mm²), at over 2.4 and 3.3 standard deviation units from the *A. africanus* and *A. afarensis* means, respectively. This specimen is considered as taxonomically indeterminate and is further discussed below. L628-10, from Member G, exhibits a robust-like crown shape with convex buccal contour and elongated distal crown. However, it is small in absolute size. Measured crown area is at the lower end of the *A. robustus* range of variation and is considerably smaller than in all other Shungura M2s allocated here to the robust category. Furthermore, it is more similar to nonrobusts in cusp proportions

and shows a wear pattern with distinct facets. We tentatively consider L628-10 to represent a nonrobust taxon.

OMO28-30 is a large M3 (measured crown area of 218 mm²), surpassed in size only by STW237 among the nonrobust specimens of the current comparative sample. It exhibits a distally projecting crown resulting in robust affinities in the canonical variate analysis of crown shape variables. Occlusal ridges are strongly inflated as in many robust *Australopithecus* M3s, but this also occurs in some *A. africanus* molars. Cusp proportions are, however, more as in nonrobust M3s, as expressed in the canonical variate analysis of the relative cusp areas or in the cusp 6 to hypoconulid ratio. Taking the generally high variability of M3s of any taxon into account, it is difficult to assess the affinities of this molar. The possibility that it represents a very early robust *Australopithecus* taxon at upper Member B times will be further examined below.

L628-2 from Member G also exhibits an unusual combination of features. It is large

TABLE 4. Allocation of relatively complete mandibular molars to robust or nonrobust categories¹

Specimen	Stratigraphic level	Taxonomic allocation	Morphological indicators of affinities						
			Crown area	Cusp proportion	Crown shape	C6	C7	Wear pattern	Enamel thickness
First molars									
OMO212-1950	B10	NR	NR	NR	NR	(R)	—	—	—
ER5431	Mid C	NR ²	—	—	—	—	—	NR	—
L45-2	C5	NR	(NR)	NR	(NR)	(NR)	—	NR	—
OMO18-34	C8	R	R	R	(R)	(R)	—	—	—
L51-1	C9	NR	—	—	NR	R	—	(NR)	—
L824-5	D1	NR	(NR)	—	—	—	(NR)	(NR)	—
WT16005	D	R ²	R	—	(NR)	—	—	R	—
L26-1g	E2	NR	—	R	(NR)	(NR)	(NR)	—	—
L628-9	G3	R	R	R	—	R	—	—	—
OMO195-1630	G7/8	NR	NR	NR	NR	—	—	(NR)	—
OMO75s-15	G1-13	NR	—	NR	NR	—	(NR)	(R)	—
OMO75-14	G13	NR ²	R	—	—	—	(NR)	NR	—
Second molars									
L795-1	B12/C1	?R/NR	R	NR	NR	—	(NR)	—	—
ER5431	Mid C	NR ²	—	(NR)	(NR)	—	(NR)	(NR)	—
L62-17	C4-6	R	—	—	(R)	—	—	(R)	—
L157-35	F1	R	R	(R)	NR	—	—	(R)	—
F22-1a	F1	R	R	(R)	—	—	—	(R)	R
OMO136-2	G1	R	—	—	(R)	R	—	(R)	—
L628-10	G3	cf. NR	—	(NR)	R	—	—	(NR)	—
L427-7	G4	R ²	—	(R)	NR	—	—	—	—
L7-279	G4-8	NR	—	NR	NR	—	(NR)	NR	—
OMO47-46	G8	R	R	(R)	R	R	—	R	R
OMO47-1500	G8	R	(R)	—	(R)	—	—	R	—
OMO75-14	G13	NR ²	R	(NR)	R	—	(NR)	NR	—
Third molars									
OMO28-30	B9/10	?R/NR	(R)	—	R	(NR)	—	—	—
L1-294	B10	NR	—	NR	—	NR	—	(NR)	—
L1-398	B10	NR	(NR)	NR	(NR)	—	—	—	—
L2-89	B10	NR	NR	NR	—	NR	—	NR	—
L296-1	D1	R	—	—	—	—	—	(R)	—
L9-11	Upper D	NR	—	NR	(NR)	(NR)	—	(NR)	—
L338x-39	E3	R	R	(R)	R	(R)	—	—	—
L398-630	F0	R	—	—	—	(R)	—	(R)	(R)
OMO33-9	F0	R	R	(R)	R	(R)	—	(R)	—
OMO33-6172	F0	R	—	(R)	—	—	—	(R)	—
L28-30	F1	NR	—	NR	(R)	NR	—	—	—
F22-1b	F1	R	R	—	—	(NR)	—	—	R
OMO136-1	G1	R	—	—	—	(R)	—	—	R
L628-2	G3	R	R	—	NR	—	—	NR	—
L628-3	G3	R	R	—	(NR)	(R)	—	—	—
L7a-125	G5	R ²	R	—	(NR)	—	—	R	—
OMO75s-16	G1-13	NR	NR	NR	—	NR	—	NR	—
OMO75-14	G13	NR ²	—	—	—	—	—	(NR)	—

¹Stratigraphic level refers to Shungura Formation terminology of de Heinzelin (1983). For ER and WT specimens, the stratigraphic correlation of Feibel et al. (1989) is followed. Taxonomic allocations are restricted to robust/nonrobust dichotomization noted as R and NR, respectively. Morphological indicators are as follows. R and NR note instances in which a specimen falls outside the known range of variation of the nonrobust and robust comparative samples, respectively. Crown area is the measured occlusal view crown area, cusp proportion is evaluated by the first canonical variate derived from analyses of five (M1 and M2) or six (M3) relative cusp areas, and crown shape is evaluated by the first canonical variate derived from seven scaled linear variables. Parentheses refer to cases in which the specimen is within the extreme three cases of the opposite comparative group. With the C6 of M1 and M2, R and NR designations indicate relative C6 area outside the known range of the other group. Parentheses indicate mere presence or absence of the C6 in the M1. In the M3, C6/hypoconulid area ratios outside the known range of the one or the other comparative sample are indicated. Parentheses note instances when a specimen falls within the overlap zones restricted by cutoff points of <0.7 and >1.0. Evaluation of the C7 consists of simply noting presence in M1 and M2. Wear pattern was evaluated by direct comparison, with NR and R designations given when wear was interpreted to be outside the known range of variation of the other comparative sample, or perhaps within a narrow zone of overlap in variation, such conditions being indicated by parentheses. Radial enamel thickness ≥ 2.4 mm, measured at the mesial, distal, or lingual crown faces, is taken as an R indication, while instances of ≥ 2.3 mm are listed within parentheses.

²Indicates availability of associated premolar and/or mandibular evidence.

in size, with an estimated crown area larger than the *A. boisei* mean and beyond the range of variation of all other taxa. However, the distal crown is not developed to the de-

gree usually seen in robust M3s, and the crown is not worn flat, retaining an occlusally projecting metaconid. Because other Member G robust M3s also exhibit an abbre-

viated distal crown, L628-2 is here considered to be a robust specimen with an unusual wear pattern.

OMO75-14 is an associated dentition consisting of mandibular and maxillary postcanine teeth with poorly preserved mandibular and maxillary osseous portions. Presumably because of its large size, this specimen has been included in the robust *Australopithecus* hypodigm by some (e.g., Wolpoff, 1988; Wood et al., 1994). Others have pointed out the reduced right and absent left M3, suggesting a *Homo* attribution (Wallace, 1977). The premolar and molar data presented here exhibit conflicting results. While the single most diagnostic element, the mandibular P3, exhibits a nonrobust morphological pattern (for details see Figure 3; Suwa, 1990), the sizes of P3 through M2 are all larger than the largest known nonrobust specimens. M2 crown shape suggests a robust pattern, while the well-developed C7 on all molars and postcanine wear pattern suggest nonrobust affinities. Thus, the balance of evidence of the mandibular teeth suggests a nonrobust status. Furthermore, it was found by one of us (G.S.) that the OMO75-14 piece reported by Coppens (1971) as a right maxillary fragment with M1 is in fact a left mandibular portion with exploded P4. This piece actually forms a true join with the adjacent mandibular pieces. Although a true midline join is still lacking, this allows a reasonable reconstruction of dental arcade shape (Fig. 6). The linear right and left arcades' converging anteriorly is reminiscent of early *Homo* mandibles (e.g., ER1802, UR501) and corroborates the above conclusion based on individual tooth crown morphology. Thus, we interpret OMO75-14 to be a large nonrobust specimen and include it as such in the subsequent analysis.

EVOLUTION OF THE ROBUST *AUSTRALOPITHECUS* LINEAGE AT OMO Timing of "robust" emergence

Since the discovery of KNM-WT 17000 (Walker et al., 1986; Leakey and Walker, 1988), the presence of a robust *Australopithecus* species in the Turkana basin at circa 2.5 myr is uncontested. More fragmentary but earlier evidence of robust-like den-

tal morphology consists of two mid-Member C specimens. One is the L55-33 fragmentary mandible preserving a partial P4. The preserved premolar morphology and wear, together with the extensive *planum alveolare*, were interpreted by Suwa (1988, 1990) to represent evidence of robust *Australopithecus* affinities. An isolated M2, L62-17, is also likely to be an early robust based on crown shape and the comparatively flat wear pattern with lack of facetting. From upper Member C, there are many specimens with more clear robust morphological affinities. These include the OMO18-31 P3, the OMO18-34 M1 and the OMO18-18 mandible. Thus, the presence of robust *Australopithecus* by Member C times is solidly documented, with the first definite appearance best estimated at mid-Member C 2.7 myr.

There is a lack of specimens from lower Member C, while a large M2 (L795-1) derives from around the B/C boundary and an M1 and four measurable M3s are known from upper Member B. There are tantalizing suggestions that some of these may represent the earliest manifestation of the robust lineage or clade. L795-1 was initially described as an M3 but is considered an M2 from both morphological criteria of the crown and root and application of discriminant function analysis (Suwa, in press). This is a large tooth exceeding known nonrobust ranges of variation in crown area and lies at the uppermost ranges of *A. robustus* M2s. It is, however, morphologically comparable to the nonrobust condition in cusp proportions, crown shape, and C7 presence. The OMO28-30 M3 also exhibits large size and a mixture of nonrobust and robust-like features, as outlined above.

It may be that we are sampling the very initial stages of robust *Australopithecus* differentiation in this association of large size and conservative molar morphology. This is an admittedly weak argument that gains some support in the extreme size range exhibited by the known mandibular molars from this time horizon. The four measurable M3s from upper Member B vary in measured crown area from 132–218 mm². The smallest specimen (L2-89) is smaller than the smallest *A. afarensis* M3 of the comparative sample, while OMO28-30 is larger than the

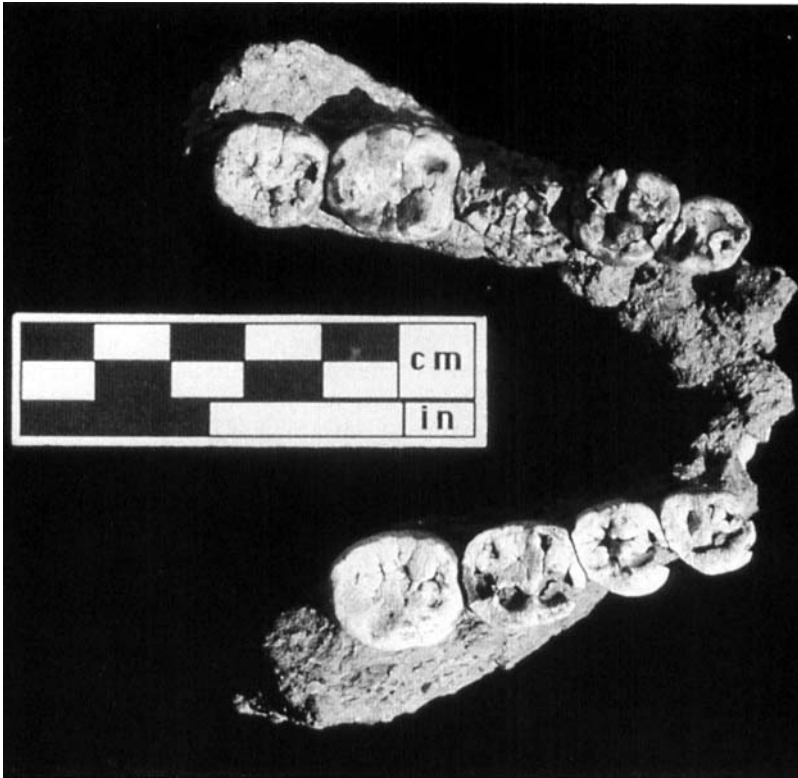


Fig. 6. The reassembled OMO75-14 mandibular specimen.

largest member of the same sample. The crown area range exhibited by the four molars is 86 with a coefficient of variation (CV) of 21.3. These values compare with ranges of 64, 96, and 91 in *A. afarensis*, *A. africanus*, and *A. robustus* M3s, respectively, and CVs of around 11–13. The *A. africanus* and *A. robustus* samples consist of moderate sample sizes of 22 each and can be used to calculate bootstrap probabilities of both sample range and CV for subsamples of four. Based on 400 iterations, probabilities of attaining a CV of 21.3 or greater were estimated to be 0.045 and 0.015 by the *A. africanus* and *A. robustus* models, respectively. Probabilities of a range of 86 or greater were calculated as 0.04 and 0.055, respectively, by use of the same two models.

These results indicate that the possibility of a taxonomically heterogeneous situation in upper Member B times is real. More lim-

ited evidence from the first two mandibular molars also supports this interpretation. The single measurable M2 (L795-1) exceeds all nonrobust maxima as already outlined above. Conversely, the single measurable M1 (OMO212-1950) is small, with the measured crown area at two standard deviation units below the *A. afarensis* mean, and equivalent to the smallest known nonrobust M1s such as of AL288-1 and AL128-23.

Morphological affinities of the Shungura Formation robusts

Further analysis of the Shungura robusts focuses on features that characterize *A. robustus* and *A. boisei*. Ideally, apomorphic features of both species should be identified and the Shungura specimens evaluated in regard to these. This is comparatively easier for *A. boisei*, whose dentition is highly derived. From the extensive analyses of premo-

Z-score

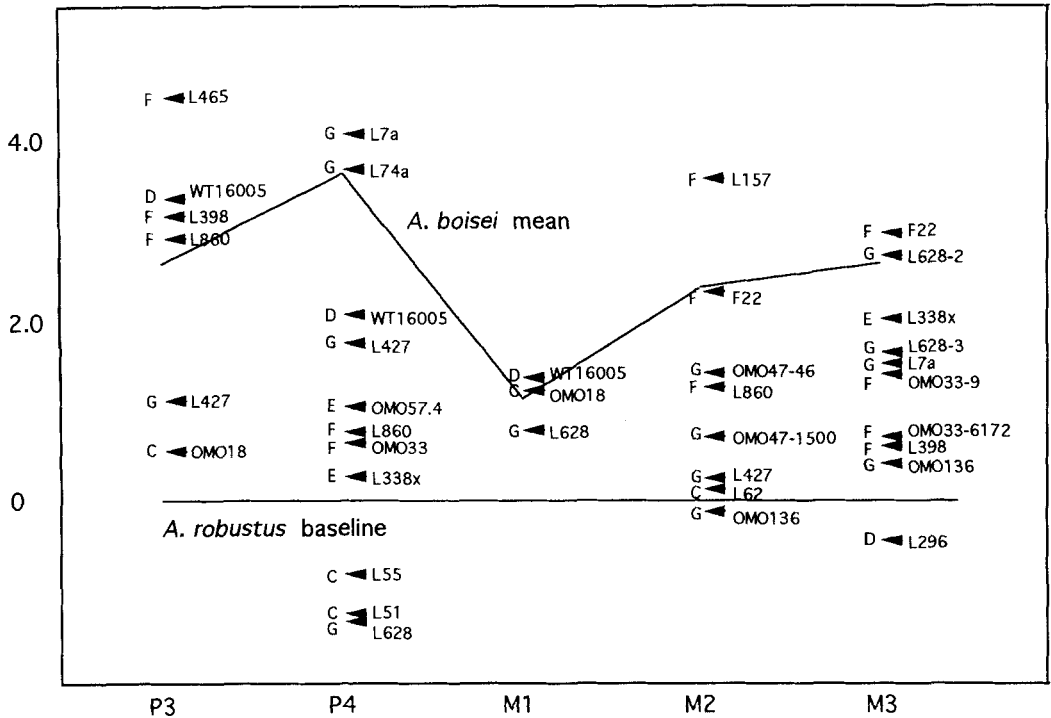


Fig. 7. Measured crown area of the Shungura robust *Australopithecus* specimens. Z-scores were calculated using the *A. robustus* means and standard deviations. Letters indicate stratigraphic level of each Omo specimen.

lars, molars, and relative dental size, we choose the following features which we interpret to be uniquely derived features/trends of post-2 myr *A. boisei*: 1) absolute size of all postcanine elements large, 2) relative size of the P4 large, 3) a distinctive P4 morphology, 4) mandibular molars with distinct cusp proportions, and 5) relative size of the anterior dentition small. The basis for these is outlined in detail in Wood and Stack (1980), White et al. (1981), Wood and Abbott (1983), Wood et al. (1983), Wood and Uytterschaut (1987), Wood (1991b), Suwa (1988, 1990) and Suwa et al. (1994) and is not repeated here. Although other less clear-cut trends do characterize either *A. robustus* or *A. boisei*, we focus our analysis on the above as the most clear features that can be evaluated by precise metric methods.

Absolute tooth size is presented in Figure

7 and Table 5. It can be seen that the Shungura specimens fall largely between the *A. robustus* and *A. boisei* means. Because sample sizes of the Shungura postcanine dentition by tooth position and stratigraphic interval are small, to facilitate interpretations, z-scores were calculated using *A. robustus* as a baseline. In this way, relative sizes of teeth from different positions can be compared together. It can be seen that the Member C robust specimens fall both above and below *A. robustus* means, while those from Member D and higher stratigraphic levels tend to be consistently larger than *A. robustus* but smaller than *A. boisei*. Further temporal trends are less clear, but overall tooth size is largest in Member F, approximating the *A. boisei* mean conditions. There is, however, no indication of a gradual increase of tooth size through time from Mem-

TABLE 5. Measured crown area of robust *Australopithecus* specimens¹

	P3 Mean	SD	P4 Mean	SD	M1 Mean	SD	M2 Mean	SD	M3 Mean	SD
<i>A. robustus</i>	88.5	9.1	116.0	12.9	168.3	20.1	199.5	22.7	197.9	26.0
<i>A. boisei</i>	112.0	16.5	162.7	24.9	191.6	19.3	252.7	36.9	267.0	53.2
Member C										
L55-33			(106)							
L51-79			99.4							
OMO18-31	93.6									
OMO18-34					193.2					
L62-17							201.6			
Member D										
L296-1									(187)	
WT16005	119.0		(143)		195.7					
Member E										
OMO33-508			123.4							
OMO57.4-41			(129)							
L338x-40			119.0							
L338x-39									250.2	
Member F										
L398-120	117.0									
L465-111	(129)									
L860-2	(115)		(125)				(228)			
L157-35							281.1			
F22-1a,b							258.6		274.9	
L398-630									(213)	
OMO33-9									234.9	
OMO33-6172									(214)	
Member G										
L427-7	99.2		(139)				202.0			
L628-4			99.3							
L7a-125	((135))		(169)						(236)	
L74a-21			163.1							
L628-9					183.8					
OMO47-1500							215.3			
OMO136-2							197.6			
OMO47-46							(232)			
OMO136-1									209.4	
L628-2									(268)	
L628-3									240.2	
	N		Mean z-score							
Member C	5		-0.03							
Member D	2		0.93							
Member E	4		0.95							
Member F	8		2.26							
Member G	11		1.25							

¹Parentheses indicate estimates; double parentheses indicate a very rough estimate. Mean z-scores were calculated from the *A. robustus* baseline. The mean z-score of *A. boisei* across tooth position is 2.47.

ber D through Member G (see also Wood et al., 1994).

Morphological specialization of the P4 in *A. boisei* has been treated extensively by Suwa (1988, 1990). The derived *A. boisei* morphology consists of small metaconid and anterior crown areas, a mesially placed metaconid relative to the mesial and distal protoconid crests, a large posterior crown area with broad talonid, a large mid-crown relative to buccal crown length, and a large length/breadth ratio. This derived morphology has been interpreted to be directly re-

lated to an enlarged talonid resulting in a disproportionately large relative P4 size compared to the *A. robustus* condition. It has been demonstrated that this morphology first appears in Member G (L427-7, L74a-21, and possibly L7a-125) and is conspicuously absent from the earlier time horizons.

Statistics on relative P4 size relevant to this study are summarized in Table 6. Three Omo specimens, L427-7, L7a-125, L860-2, and WT 16005 can be evaluated relative to the *A. boisei* and *A. robustus* conditions. It can be seen that of these four specimens only

TABLE 6. Relative size of mandibular P4

	N	P4 area/M1 area		
		Mean	SD	Range
Nonrobust	22	.628	.050	.522-.705
<i>A. robustus</i>	12	.683	.068	.538-.769
<i>A. boisei</i>	4	.834	.042	.779-.875
WT16005 (D)		.73		
	N	P4 area/M2 area		
		Mean	SD	Range
Nonrobust	21	.529	.041	.465-.610
<i>A. robustus</i>	9	.569	.053	.466-.612
<i>A. boisei</i>	7	.671	.049	.594-.726
L860-2 (F)		.55		
L427-7 (G)		.69		
	N	P3 area/P4 area		
		Mean	SD	Range
Nonrobust	25	.899	.057	.789-1.013
<i>A. robustus</i>	6	.784	.078	.713-.912
<i>A. boisei</i>	3	.675	.037	.637-.711
WT16005 (D)		.83		
L860-2 (F)		.92		
L7a-125 (G)		.80		
L427-7 (G)		.71		

L427-7 from Member G approximates the derived *A. boisei* condition, while the two specimens from lower stratigraphic levels exhibit the more generalized proportion.

Relative anterior dental size can be evaluated in L74a-21, L7a-125, OMO57.4-14, WT16005, and L55-33 (Table 7). Although the comparative data base is small because of the paucity of specimens with both measurable anterior and posterior dentition, the current results are highly suggestive and are presented here as a starting point for further data collection and analyses. Relative canine size in L74a-21 exhibits proportions closer to the *A. robustus* condition than to that of *A. boisei*, while L7a-125 shows an intermediate condition. This is the case despite the large premolars of these specimens and suggests a comparatively larger canine than seen in later *A. boisei* specimens. As another measure of relative anterior dental size, canine to incisor alveolar length was evaluated relative to postcanine crown area. In these measures, specimens from Member E and lower stratigraphic levels (OMO57.4-41, WT16005, L55-33) exhibited conservative values comparable to or more primitive than the *A. robustus* condition, while the L7a mandible showed *A. boisei* proportions. Comparable metrics on the maxillary denti-

TABLE 7. Relative size of the mandibular canine and anterior alveolar length

	N	Canine breadth/P3 area square root		
		Mean	SD	Range
Nonrobust	18	1.101	.112	.917-1.415
<i>A. robustus</i>	3	.873	.046	.824-.914
<i>A. boisei</i>	4	.841	.036	.802-.874
L7a-125 (G)		.84		
	N	Canine breadth/P4 area square root		
		Mean	SD	Range
Nonrobust	13	1.031	.078	.897-1.168
<i>A. robustus</i>	4	.792	.111	.691-.949
<i>A. boisei</i>	3	.683	.049	.640-.737
L7a-125 (G)		.75		
L74a-21 (G)		.77		
	N	I1-C alveolar LT/P3 area square root		
		Mean	SD	Range
Nonrobust	12	2.033	.135	1.768-2.273
<i>A. robustus</i>	2	1.739	.000	1.739-1.739
<i>A. boisei</i>	2	1.525	.030	1.504-1.546
WT16005 (D)		1.76		
L7a-125 (G)		1.42		
	N	I1-C alveolar LT/P4 area square root		
		Mean	SD	Range
Nonrobust	11	1.923	.136	1.630-2.092
<i>A. robustus</i>	3	1.497	.031	1.469-1.531
<i>A. boisei</i>	3	1.279	.076	1.234-1.366
L55-33 (C)		1.65		
WT16005 (D)		1.61		
OMO57.4-41 (E)		1.45		
L7a-125 (G)		1.26		

tion show a similar generalized condition in the relative canine size of the OMO323 cranium from Member G (Suwa, 1990) and in the relative anterior alveolar length of WT17000 (Suwa, 1989).

Finally, relative cusp size of the mandibular molars was evaluated in relation to results of principal components analysis presented in Suwa et al. (1994). In all three molars the first axis expresses differential talonid development, with *A. boisei* exhibiting the more extreme cusp proportions relative to the *A. robustus* condition. The Omo teeth were evaluated a posteriori in this comparative framework. It can be seen that the Shungura robust *Australopithecus* collection as a whole does not approximate the *A. boisei* condition, regardless of stratigraphic level (Fig. 8). In particular, the Member G speci-

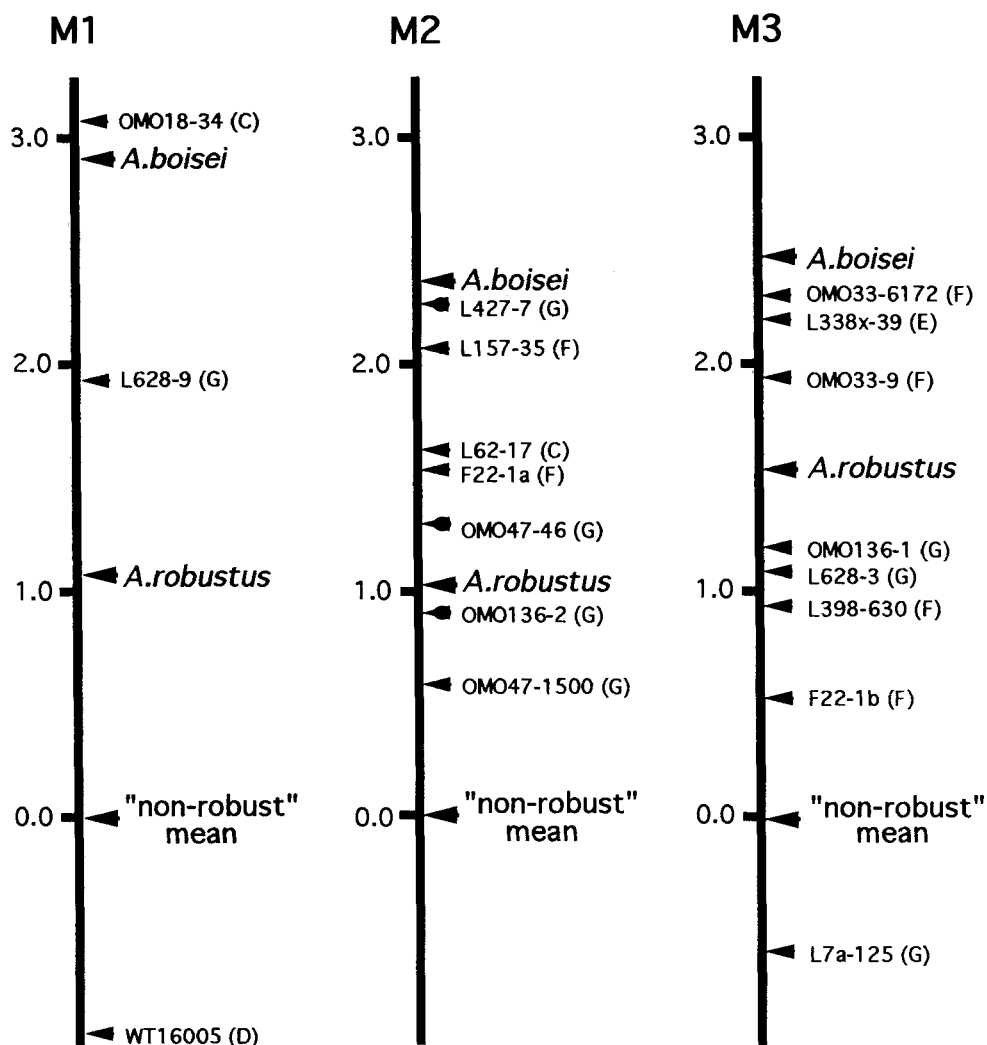


Fig. 8. First axis scores of the principal components analysis of five (M1 and M2) or six (M3) relative cusp areas of the mandibular molar. Large positive values indicate molar crowns with relatively large distal cusps. See Suwa et al. (1994) for further details of the principal components. Values are z-scores from the nonrobust mean. Letters indicate stratigraphic level of each Omo specimen.

mens failed to exhibit *A. boisei* tendencies in all three molar positions.

In another more direct evaluation of measured cusp areas, relative posterior crown size was tabulated as the combined entoconid, hypoconulid, and cusp 6 areas (Table 8). This produces a measure of posterior crown size robust to interobserver error (Suwa et al., 1994) and thus may be of use in a wide context. It can be seen that most of the 18 mandibular molars cluster around

the *A. robustus* mean, with only four Omo specimens (one each from Member C, E, F, and G) falling close to the *A. boisei* mean. As in the principal components analysis, the Member G specimens failed to exhibit any approximation to the *A. boisei* pattern.

Thus, with the five defining features/trends of the *A. boisei* dentition, acquisition of the derived condition by the East African robust lineage is seen in a mosaic pattern. The robust specimens from Member C

TABLE 8. Relative posterior cusp size of mandibular molars, sum of hypoconulid and entoconid areas divided by crown area

	N	Mean	SD	Range
M1				
<i>A. robustus</i>	20	.360	.017	.329-.381
<i>A. boisei</i>	6	.394	.030	.352-.428
C-G average	3	.355	.044	.310-.397
OMO18-34 (C)		.397		
WT16005 (D)		.310		
L628-9 (G)		.357		
M2				
<i>A. robustus</i>	16	.353	.017	.325-.380
<i>A. boisei</i>	9	.376	.020	.351-.410
C-G average	7	.359	.011	.337-.372
L62-17 (C)		.337		
L157-35 (F)		.364		
F22-1a (F)		.357		
L427-7 (G)		.365		
OMO47-46 (G)		.364		
OMO47-1500 (G)		.372		
OMO136-2 (G)		.353		
M3				
<i>A. robustus</i>	20	.369	.031	.310-.414
<i>A. boisei</i>	8	.421	.022	.372-.440
C-G average	8	.366	.046	.303-.431
L338x-39 (E)		.417		
L398-630 (F)		.335		
F22-1b (F)		.387		
OMO33-9 (F)		.386		
OMO33-6172 (F)		.431		
L7a-125 (G)		.331		
L628-3 (G)		.303		
OMO136-1 (G)		.335		

through F do not exhibit any approximation to the advanced *A. boisei* condition, except in large absolute size seen in specimens from Members D through F. However, overall dental size does not match the *A. boisei* condition. The conspicuous morphological specialization of the P4 and its large relative size clearly appears first in Member G times, although one Member G P4, L628-4, exhibits the more generalized condition (Suwa, 1988, 1990). At the same time, the advanced *A. boisei* condition seems to be only partially attained in relative anterior dental size. Finally, in mandibular molar cusp proportions, the Omo robust specimens retain the conservative condition throughout their known distribution extending to middle Member G times.

Discussion

There is some evidence that an incipient robust taxon was emerging at B/C times at circa 2.9 myr. This suggestion is based solely on the six measurable mandibular molars

available at present and must be tested by further more diagnostic fossil remains.

The robust specimens from Members C to F can be allocated to *A. aethiopicus* and are largely plesiomorphic for robust *Australopithecus* in the major features of their dentition. These dentitions are, however, more derived than *A. robustus* in larger size. This can be interpreted in two ways. One hypothesis would consider larger postcanine size to be a shared derived feature of *A. boisei* and *A. aethiopicus*. This would mean that the common ancestral stock of the East and South African robusts must have existed at or before Member C times. This hypothesis would be concordant with a polyphyletic emergence of robust *Australopithecus*, with *A. robustus* evolving from *A. africanus* in southern Africa.

An alternative possibility, consistent with robust *Australopithecus* monophyly, would necessitate a reduction in overall dental size to have occurred concurrent or subsequent to the cladistic event that formed *A. robustus*. With this latter hypothesis, the dental evidence constrains the timing of the separation to have taken place at or prior to lower Member G times, while cranial evidence such as WT17000 (Leakey and Walker, 1988; Kimbel et al., 1988) and L338y-6 (Rak and Howell, 1978; Holloway, 1981; Howell et al., 1987) would set the date to post-Member E times. This gives a circa 2.4 to 2.3 myr estimate for the phyletic split leading to the South African *A. robustus*. Viewed in a zoogeographic context, a scenario where the East African robust *Australopithecus* species expanded its range of distribution southward at this time and then became isolated from those parent populations is appropriate. Dental size reduction may have occurred through genetic drift or as part of some selective regime coupled with smaller body size.

The Shungura robust specimens from Member G exhibit a mixture of *A. boisei*-like and less derived character states. This mosaic pattern of derived morphological features and dental proportions seen in the Member G specimens suggests both evolutionary continuity from earlier stratigraphic levels and in situ evolution of the robust lineage during Member G times. This can be

taken as evidence for refuting Skelton and McHenry's (1992) assertion that *A. aethiopicus* has no relationship with *A. boisei*. At present, no clear temporal pattern can be discerned within Member G. We hypothesize that an in situ anagenetic transformation in the dentition of the East African robust lineage took place across Member G times.

These results are in agreement with those already put forward by Howell et al. (1987), Suwa (1988), and Wood et al. (1994) in recognizing a less derived robust *Australopithecus* species prior to Member G times. It has become apparent from the current study, however, that the Member G robust specimens do not possess all of the derived dental features characteristic of later *A. boisei*. This seemingly mosaic nature of evolutionary change leading to the post-2 myr *A. boisei* condition precludes an entirely satisfactory definition of an *A. aethiopicus/boisei* boundary, especially since the nature of this transition is not presently well documented. It is perhaps appropriate for the time being, then, to allocate all Member G specimens to *A. aff. boisei* as the earliest member of this species (except perhaps the L628-4 P4) because the lower Member G sample exhibits at least some of the more clear *A. boisei* dental features while also exhibiting *A. boisei*-like mandibular dimensions (Wood et al., 1994) and a partially advanced set of cranial features (Rak, 1983; Coppens and Sakka, 1983).

AFFINITIES AND EVOLUTION OF THE NONROBUST LINEAGE

Premolar morphology and the emergence of *Homo*-like features

Mandibular premolar and molar features that characterize the three nonrobust taxa are more subtle. Comparatively clear trends occur in mandibular P3 morphology and in molar shape (White et al., 1981). Suwa (1990, 1991) has shown that an *A. afarensis* to *A. africanus* to *Homo* morphocline can be proposed in the evolution of mandibular P3 morphology. From a wider set of variables, eight features were identified as shared derived trends of *A. africanus/Homo*, and another eight were considered to be uniquely derived trends of early *Homo* (Table 9). These features mostly relate to the progres-

TABLE 9. Derived features of *A. africanus* and early *Homo* mandibular P3s relative to the *A. afarensis* condition¹

Derived features/trends common to both <i>A. africanus</i> and early <i>Homo</i>
Mesiolingual contour with transverse component (MLINGCNT)
Distolingual contour rounded and obtuse (DLINGCNT)
Major crown axis in occlusal view only weakly oblique (OBLQANG)
Lack of mesioinferior projection of buccal cervical line (EDJMBUCP)
Lingual segment of mesial marginal ridge always present (MMRLING)
Transverse crest only moderately prominent (TRCRST)
Metaconid distinctly developed (MDINDIV)
Metaconid slightly mesially placed relative to protoconid (MDANG)
Uniquely derived features/trends of early <i>Homo</i>
Basal contour of buccal crown not asymmetric (BASBUCAS)
Crown not elongated in oblique major axis direction (LTBRNDXE)
Mesial marginal ridge moderately high (MMRHT)
Lingual segment of mesial marginal ridge well developed (MMRLING)
Metaconid sometimes low relative to marginal ridges (MDINDIV)
Metaconid more mesially placed relative to protoconid (MDANG)
Longitudinal groove angled mesiobuccally (LONGANG)
Distal buccal groove weak or lacking (DISBUCGR)

¹ Corresponding variable names are in parenthesis. See Suwa (1990) for details.

sive loss of primitive features retained from a sectorial P3 ancestry. However, considerable within-taxon variation exists, with individual exceptions frequently occurring in these general trends.

Because any evaluation of the Omo dentition in these features must take this inherent degree of variation into account, all variables were first converted to categorical status, and then a multidimensional scaling analysis was performed to express the range of variation within each taxon. These results are exhibited in Figures 9 and 10. It can be seen that up to one-third of *A. afarensis* specimens exhibit the *A. africanus/Homo* derived trends, while two of 15 *Homo/A. africanus* P3s show the more primitive condition frequent in *A. afarensis*. Regarding the additional derived trends of early *Homo*, only one of 21 *A. afarensis/africanus* P3s exhibited this morphology, while one-fourth of the early *Homo* sample retained the primitive condition.

Turning to the seven nonrobust specimens from Member C through G, it is clear that,

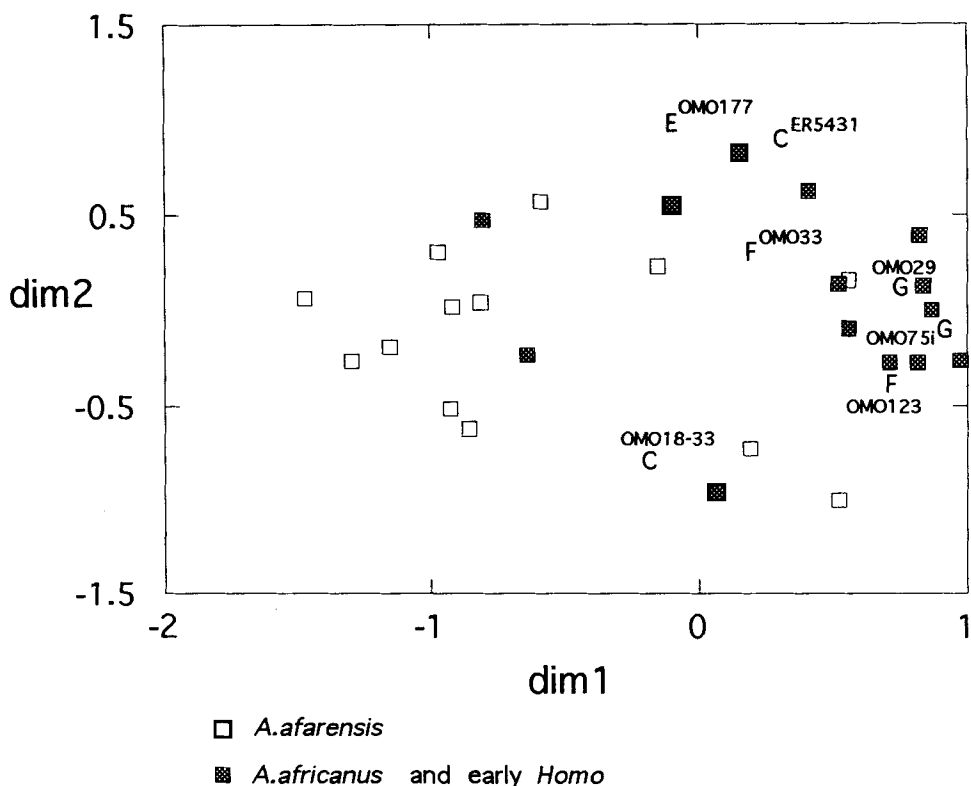


Fig. 9. Multidimensional scaling analysis of eight variables listed in Table 9 to be shared derived features/trends of the mandibular P3 of *A. africanus* and early *Homo*. Input variables are MLINGCNT, DLINGCNT, OBLQANG, EDJMBUCP, MMRLING, TRCRST, MDINDIV, and MDANG. The categorical variables were dichotomized by presence/absence of the derived *A. africanus*/early *Homo* modal condition (except for MMRLING which was dichotomized just by presence/absence of the feature itself). The continuous variables OBLQANG and MDANG were converted to categorical

status using the midpoint of the *A. afarensis* and *A. africanus* means as the boundary. The first axis tends to segregate *A. afarensis* from *A. africanus*/early *Homo*, with Kendall's coefficients of rank correlation ranging from 0.4–0.7 for all variables except OBLQANG. This indicates a tendency for *A. africanus* and early *Homo* P3s to exhibit a less asymmetric crown contour in occlusal view, a weaker, more incised trigonid crest, a better developed mesial marginal ridge, and a slightly mesially placed metaconid. Letters indicate plot position and stratigraphic level of each Omo specimen.

as a group, these P3s unambiguously exhibit a derived condition distinct from the *A. afarensis* condition. In particular, the five specimens from the circum 2.4 to 2.0 myr time interval approximate the early *Homo* condition in tending to exhibit a less asymmetric crown with better developed mesial marginal ridges compared to the *A. afarensis* or *A. africanus* conditions. Only two mandibular P3s are known from the earlier horizons, with a 2.6–2.7 myr age. These specimens incompletely exhibit the advanced *Homo* condition. In the multidimensional scaling analysis, ER5431 failed to show the derived

Homo condition, while OMO18-33 only incipiently exhibited the derived *A. africanus*/*Homo* features.

Molar shape and transition from the *A. afarensis* condition

The shape of M1 and M2 in *A. afarensis* has been described as bilobed in occlusal view and with a mesially "appressed" hypoconulid (White et al., 1981). This is expressed by the linear variables of the present study, which in multivariate form exhibit a strong tendency to segregate *A. afarensis* molars from those of *A. africanus*/*Homo*.

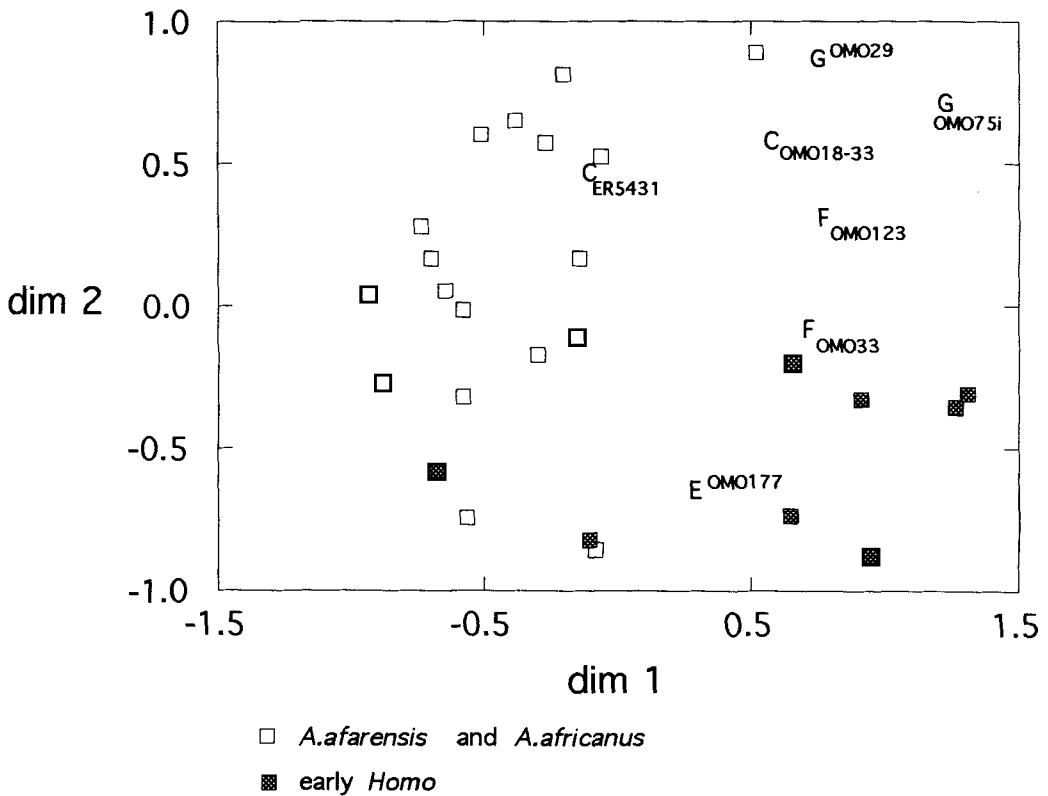


Fig. 10. Multidimensional scaling analysis of eight variables listed in Table 9 to be uniquely derived features/trends of early *Homo*. Input variables are BASBUCAS, LTBRNDXE, MMRHT, MMRLING, MDINDIV, MDANG, LONGANG, and DISBUCGR. The categorical variables were dichotomized by the presence/absence of the derived early *Homo* modal condition. The continuous variables LTBRNDXE, MDANG, and LONGANG were converted to categorical status using the midpoint of *A. africanus* and early *Homo* means as the boundary. The first axis tends to segregate *A. afarensis/africanus* from early *Homo* and relates predominantly to variables

MMRHT, MMRLING, LTBRNDXE, and MDINDIV, with Kendall's coefficients of rank correlation ranging from 0.4–0.7. This indicates the tendency for early *Homo* P3s to exhibit a well-developed mesial marginal ridge, a relatively narrow crown along its oblique axis, and weak metaconid expression. Axis 2 relates predominantly to variables DISBUCGR and LONGANG with coefficients of over 0.6 and 0.4, respectively. A large axis 2 score indicates a tendency for a well-developed distal buccal groove. Letters indicate plot position and stratigraphic level of each Omo specimen.

The nonrobust Omo M1s from Members B through D show intermediacy between the *A. afarensis* and *A. africanus/Homo* conditions. These are expressed in the first axis scores of the principal components analysis (Fig. 11). A large positive value in the first component score indicates a broad and mesiodistally short crown with abbreviated distal portion, as often strongly expressed in *A. afarensis* molars. The three M1s from Member C fall at the narrow interval of overlap in ranges of *A. africanus* and *A. afarensis* variation or just beyond the range exhibited

by the current small *A. afarensis* sample. Later specimens from Members E and G tend to be distributed further from the *A. afarensis* condition. The second component reflects relative breadths of the anterior and posterior crown, although no significant differences in factor scores were observed among the *A. afarensis*, *A. africanus*, and early *Homo* first molars. The third axis mostly concerns the bilobed crown profile in occlusal view as best represented by some of the *A. afarensis* molars. None of the Shungura specimens approximate the ex-

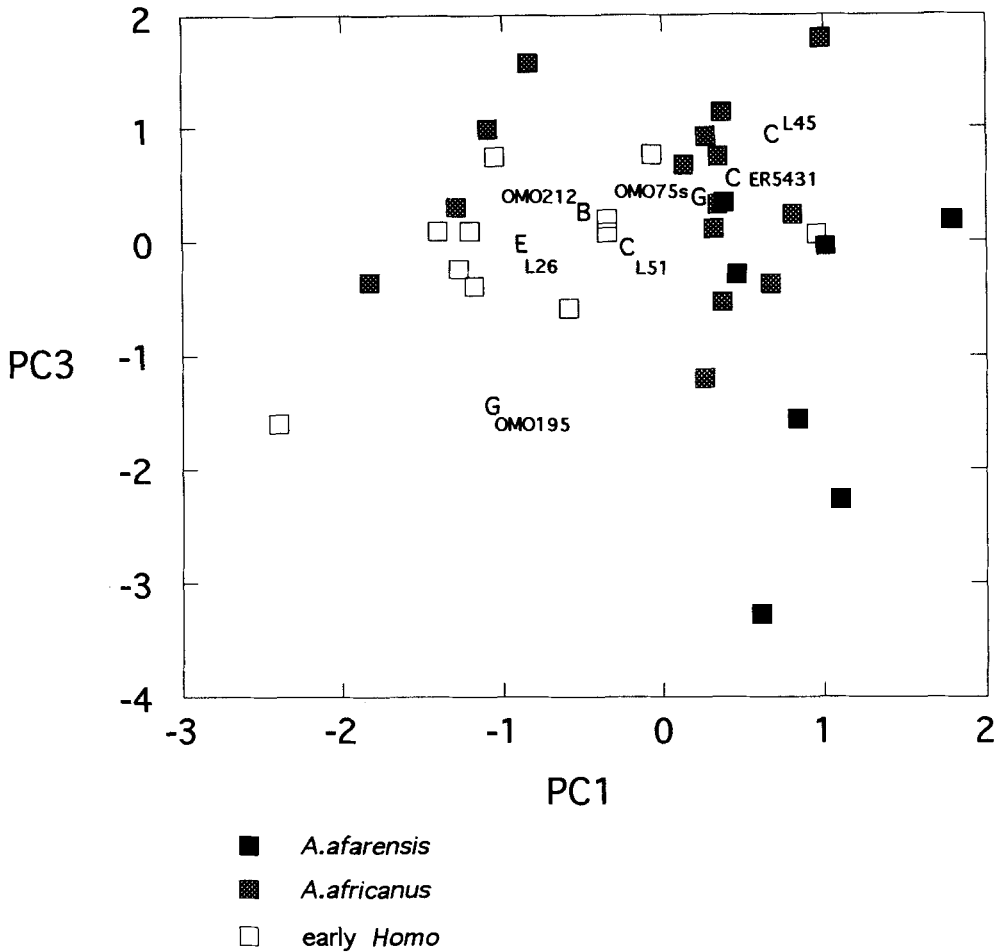


Fig. 11. Principal components analysis of seven scaled linear variables of the mandibular first molar. The raw scaled variables were used without logarithmic transformations. Only specimens with all seven variables measured or estimated were included. A large positive score in the first axis indicates a broad and mesiodistally short crown with abbreviated distal portion. See text for further details. Letters indicate plot position and stratigraphic level of each Omo specimen.

treme condition seen in some of the Hadar *A. afarensis* molars.

From a more simple evaluation of crown shape, Tobias (1966, 1991a) has repeatedly emphasized that buccolingually narrow premolars and molars are characteristic of *Homo habilis* at Olduvai. Wood (1991b, 1993) also included narrowness of cheek teeth in his definition of *H. habilis sensu stricto* but not in characterizing *H. "rudolfensis"*. In contrast, White et al.'s (1981) metric evaluation of a mixed sample of early *Homo* revealed a distinct narrowing only in

the mandibular M1, this difference seemingly stemming from variance in sample composition. Our present comparative data, also based on a mixed early *Homo* sample, are in concordance with the White et al. (1981) study. Thus, we here consider buccolingual narrowness of the M1 as a morphological indicator of general affinities with early *Homo*. Maximum crown breadth scaled by the square root of crown area is given in Table 10. It can be seen that the Members B through D nonrobust M1s equate the lower and midrange of *A. afarensis* and *A. afri-*

TABLE 10. Relative crown breadth of the mandibular first molar

	N	Maximum crown breadth/ square root of crown area		
		mean	sd	range
<i>A. afarensis</i>	14	1.052	.019	1.019–1.082
<i>A. africanus</i>	19	1.034	.017	.995–1.066
Early <i>Homo</i>	15	1.007	.024	.970–1.063
B–D average	5	1.032	.014	1.013–1.048
OMO212-1950 (B)		1.013		
L45-2 (C)		1.048		
L51-1 (C)		1.025		
ER5431 (C)		1.040		
L824-5 (D)		1.034		
E/G average	3	1.008	.012	.997–1.021
L26-1g (E)		1.007		
OMO75s-15 (G)		1.021		
OMO195-1630 (G)		.997		

canus variation, respectively, and tend to be less narrow than the early *Homo* sample of the present study. In contrast, the three M1s from Members E through G fall around the early *Homo* mean. Although variation within taxa cautions against far reaching conclusions, these results corroborate the above evidence of the mandibular P3 in demonstrating the occurrence of a more *Homo*-like M1 crown shape in the upper Shungura levels.

Absolute postcanine tooth size of the Omo nonrobusts

Mean absolute crown size of the mandibular postcanine dentition is indistinguishable between *A. afarensis* and the mixed early *Homo* sample of the present study. *A. africanus* has significantly larger mean M2 and M3 crowns, but this is not the case for P3 to M1 resulting in a different pattern of molar size proportions along the tooth row (Suwa et al., 1994). Measured crown areas of the Shungura nonrobust specimens are summarized in Table 11. In order to facilitate evaluations of the small samples of the Omo collection, z-scores were calculated with the *A. afarensis* means and standard deviations as the baseline (Table 11; Fig. 12). It can be seen that the Shungura nonrobust specimens exhibit a tendency for a large P3 through M1 dental size. Average z-scores tend to be positive regardless of stratigraphic interval, except in Members B and D, where only single specimens were available for measurement. The Shungura M2s and M3s are intermediate in size between

the *A. afarensis* and *A. africanus* conditions. With the limited number of specimens from each member, size change through time cannot be evaluated. In summary, with the currently available samples, it cannot be determined whether or not an *A. africanus* pattern of molar size proportions characterized the nonrobust lineage of eastern Africa at any time horizon.

OMO75-14 exhibits extraordinary postcanine size accompanied by M3 reduction. In particular, the three measured nonrobust M1s from Member G exhibit a CV in crown area of 20.4 and a range of 64.2. This size variation raises the possibility of taxonomic heterogeneity of the Member G nonrobust sample. Thus, bootstrap probabilities of sampling such a large size discrepancy were calculated as above using the moderately sized *A. africanus* M1 collection as a reference. Probabilities of 0.175 and 0.15 were obtained for the above CV and range values, respectively. Thus, despite the conspicuous size difference between OMO75-14 and the small OMO195-1630 M1, it can be said that this does not necessarily support a heterogeneous nonrobust taxonomic representation in Member G times.

Discussion

The nonrobust specimens from Member B of the Shungura Formation are difficult to interpret because of a lack of the more diagnostic P3s and the possible presence of an incipient robust *Australopithecus* form as suggested by the posterior molars. Omitting the two large specimens of doubtful affinity, the remaining three M3s and single M1 as a group exhibit an overall size distribution more comparable to the *A. afarensis* than *A. africanus* conditions. At the same time, the single M1 exhibits a crown shape closer to the *A. africanus* or early *Homo* condition than to that of *A. afarensis*. With such subtle evidence based on small samples, no definitive assessment of their affinity is possible at this moment.

Turning to middle/upper Member C times, the handful of molars and premolars suggests that a nonrobust taxon with a more derived morphology than is common in *A. afarensis* was present by circa 2.7 to 2.6 myr. We predict that the circa 2.9 to 2.7 myr time range is likely to be the transitional period

TABLE 11. Measured crown area of the nonrobust specimens¹

	P3		P4		M1		M2		M3	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
<i>A. afarensis</i>	79.1	12.7	86.6	10.9	140.4	15.0	158.8	22.7	161.0	17.6
<i>A. africanus</i>	82.7	9.5	93.5	10.0	145.3	19.3	190.5	18.1	186.5	24.2
Early <i>Homo</i>	77.4	10.3	86.5	12.9	134.5	16.6	158.8	18.9	155.5	21.9
Member B										
OMO212-1950					110.5					
L1-294									196.5	
L1-398									162.7	
L2-89									132.3	
Member C										
ER5431	92.9		114.0		161.1		208.9			
OMO18-33	97.7									
L51-80			80.5							
L45-2					128.9					
L51-1					148.1					
Member D										
L824-5					131.2					
L9-11									(182)	
Member E										
OMO177-4525	95.8									
L26-1g					162.4					
Member F										
OMO33-5496	83.7									
OMO123-5495	90.5									
L28-30									169.1	
Member G										
OMO29-43	92.1									
OMO75i-1255	(91)									
OMO75-14	(109)		(124)		189.0		228.1		183.3	
OMO75s-15					160.1					
OMO195-1630					124.8					
L7-279							179.8			
L628-10							171.3			
OMO75s-16									138.3	
Mean z-scores										
	N				P3-M1		N		M2/M3	
Member B	1				-1.99		3		0.59	
Member C	5				0.46		1		2.21	
Member D	1				-0.61		1		1.19	
Member E	2				1.40					
Member F	2				1.63		1		0.46	
Member G	5				1.05		4		0.59	

¹Parentheses indicate estimates. Z-scores were calculated from an *A. afarensis* baseline.

when evolution occurred from an *A. afarensis*-like to a more advanced species. The available evidence suggests that this taxon was close in overall dental morphology to the *A. africanus* condition but also mostly within the *A. afarensis* and/or early *Homo* ranges of variation. The subtle nature of the evidence based on tiny samples, however, does not allow definite statements as to affinities, and it is best at present to allocate these to *Australopithecus/Homo* with the species indeterminate.

The Members E through G nonrobust specimens with morphological similarities to the early *Homo* condition in P3 and M1 almost certainly represent an ancestral seg-

ment of the *Homo* lineage and are referable to aff. *Homo* sp. indet. From the low frequency of small specimens out of a combined position sample of 13 (only two are smaller than the early *Homo* mean), it seems likely that dental size was large in this ancestral segment of the *Homo* lineage. However, this occurs throughout the postcanine dentition and not specifically in the two posterior molars. Thus, despite the Hunt and Vitzthum (1986) analysis, dental size cannot be set forth as evidence for the presence of *A. africanus* in eastern Africa. There are other indications that suggest that *A. africanus* is not present. Three mandibular nonrobust M1s, deriving from Members D (L824-5) and G

Z-score

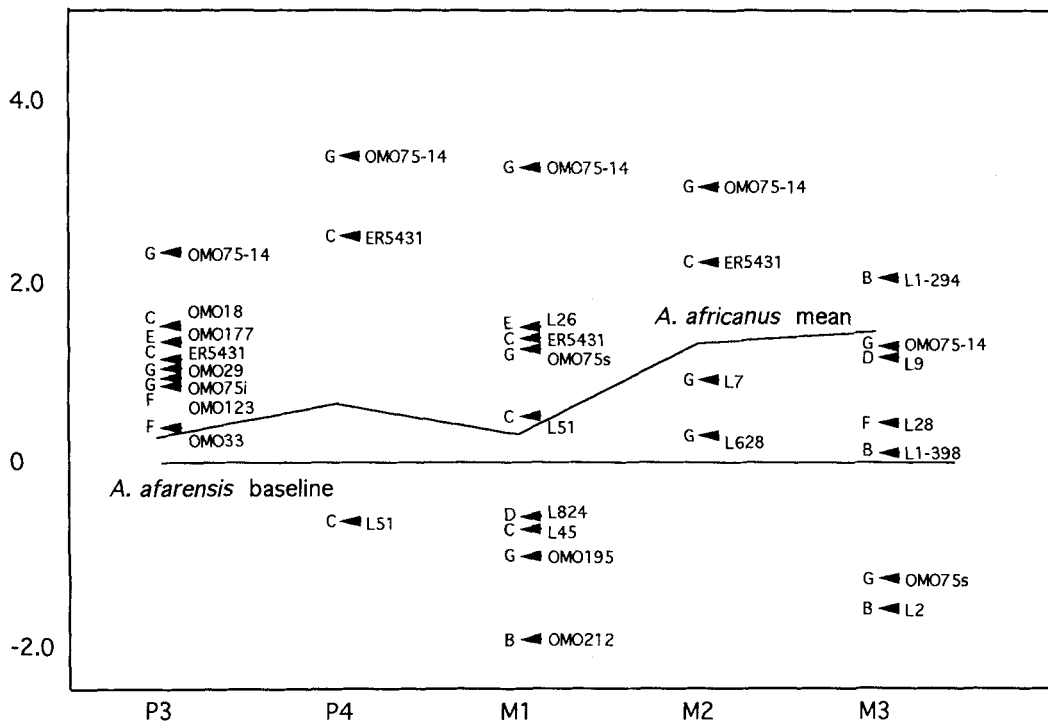


Fig. 12. Measured crown area of the Shungura nonrobust specimens. Z-scores were calculated using the *A. afarensis* means and standard deviations. Letters indicate stratigraphic level of each Omo specimen.

(OMO75s-15, OMO195-1630), as well as another likely nonrobust molar from Member C (L362-14) preserve their roots. Three of these exhibit the distinct serrated root pattern described for *A. afarensis* but not for *A. africanus* (Ward and Hill, 1987), with the remaining molar from Member G showing this pattern weakly. Thus, the presence of *A. africanus* in the Shungura Formation is contradicted by this line of evidence.

Wood (1991b, 1992, 1993) has put forward the opinion that *Homo "rudolfensis"*¹ is char-

acterized by some independently acquired robust-like features. He has noted its large dental size, developed premolar talonids, molarized P3 and P4 roots, and thicker enamel. Bromage et al. (1995) attributed the Malawi mandible UR501 to *H. "rudolfensis"* based on similarities with ER1802, specifically noting large dental size, plate-like premolar roots, P3 talonid size, and certain features of enamel microstructure. Within this context, the Shungura nonrobust lineage predominantly exhibits features that would suggest a *H. "rudolfensis"* affinity as opposed to a *H. habilis sensu stricto* attribution. Aside from large size, these features include strong development of the mesiobuccal root of the P3s, moderately developed P3 talonids with a distinct distobuccal groove, and flatter occlusal wear in both molars and premolars (Suwa, 1990). In the metric expression of crown proportions of the P3, both ER1802

¹Like Wood (1991b, 1993) and many other authors, we acknowledge substantial morphological variation in the circa 2.0 to 1.7 myr early *Homo* hypodigm traditionally allocated to *H. habilis*. However, we are presently not convinced that the suggested morphotypes actually represent specific distinctions, and hence the expression "rudolfensis." We argue below that an anagenetic model is viable regarding the dental evidence, in which case a "single species solution" (e.g., Wood, 1991b, 1993) is not out of the question. Discussion incorporating the cranial evidence is needed but beyond the scope of the present paper.

and the Shungura nonrobust specimens fell toward the end of the entire nonrobust range of variation and approximated the robust condition, as revealed in the first axis scores of the principal components analysis (Fig. 2). Among all nonrobust P3s considered in the present study, ER1802 exhibited the largest PC1 value, while all three *H. habilis sensu stricto* specimens (OH7, OH13, OH16) yielded first axis scores smaller than the post-Member D aff. *Homo* P3s. Of the four Omo P3s with sufficiently preserved roots, an advanced molarized condition is seen in OMO18-33 (Coppens, 1970; Wood et al., 1988; Suwa, 1990), and a broad and plate-like but buccally fused mesial root occurs in OMO123-5495, OMO33-5496, and OMO75i-1255 (see Coppens, 1973b; Appendix). Finally, in OMO75-14, both P3 and P4 talonids are well-developed, approximating the ER1802 condition, although quantification is difficult because of wear.

However, in the single Omo specimen which preserves both M2 and M3 (OMO75-14), the second molar is larger than the third. A reduced M3 was considered by Wood (1991b, 1993) to be characteristic of *H. habilis sensu stricto* and not of *H. "rudolfensis"*. This apparent contradiction to the otherwise *H. "rudolfensis"*-like morphology of the Shungura aff. *Homo* specimens is likely to stem from polymorphism in relative size of the M3 within early *Homo*. If this were the case, then its utility for a differential diagnosis of *H. "rudolfensis"* and *H. habilis sensu stricto* becomes unclear. In these considerations, we note that the available sample of *H. "rudolfensis"/H. habilis sensu stricto* is small. Specimens preserving both mandibular M2 and M3 crowns are confined to one in *H. "rudolfensis"* and three in *H. habilis sensu stricto* by Wood's (1991b, 1993) allocations. Of these specimens, the single *H. "rudolfensis"* example (ER1802, using an estimated area in M3) exhibits approximately subequal measured crown areas of the two molars, while *H. habilis sensu stricto* specimens OH16 and OH13 possess M2 > M3 and M2 < M3 crown area relations, respectively.

In considering the post-2 myr evidence, Wood (1991b, 1992, 1993) suggested a sister taxon relationship of *H. habilis sensu stricto* and *H. "rudolfensis"*. At the same time he

noted that these taxa were largely contemporary. The predominance of *H. "rudolfensis"*-like features in the Shungura nonrobust lineage would suggest an alternative, a time-successive relationship whereby the early *Homo* lineage initiated with a more heavily built postcanine dentition in contrast to the *H. habilis sensu stricto* condition (i.e., the *H. "rudolfensis"* dental condition is plesiomorphic). Although this observation does not contradict a *H. "rudolfensis"/habilis* sister taxon relationship, it opens up the possibility that the *H. habilis sensu stricto* specimens merely represent one end of the variation of the post-2 myr *Homo* lineage, which was undergoing a gracilization process in an anagenetic mode.

Although Wood's scheme is based on the assumption of contemporaneity of at least two early *Homo* morphotypes at Koobi Fora, we take the position that this is not sufficiently demonstrated for *H. habilis"/"rudolfensis"*, except in the temporally delimited circum KBS times. It should be noted that while the hypothesis of synchronicity of the two early *Homo* species was considered by Wood (1991b, 1993) to be most likely, the same author also carefully stated that other hypotheses (time-successive species or single taxon solution) could not be confidently falsified by the available data set. Nearly all Koobi Fora specimens allocated by Wood (1991b, 1993) to *H. habilis* or *H. "rudolfensis"* derive from the 1.85–1.9 myr interval by the Feibel et al. (1989) time scale. The only exceptions to this are the fragmentary cranium ER3891 having a less constrained provenience of 1.7–1.85 myr and the ER819 weathered mandibular corpus lacking tooth crowns provenienced at 1.6 myr, both attributed to *H. "rudolfensis"*. The poor preservation state of the latter specimen makes its allocation to *Homo* "somewhat tentative" (Wood, 1991b), and even allows a history of previous inclusion in *A. boisei* (White, 1977; Howell, 1978; Chamberlain and Wood, 1985). If it is true that temporal overlap in the two early *Homo* morphotypes was actually restricted, it then can be argued that the observed dental pattern can be explained by a significant acceleration in a gracilization process of the postcanine dentition occurring at upper Burgi Member times. We

point out that this anagenetic model is a viable alternative in respect to the dental evidence and thus should be evaluated on its own merit. This dental evidence may be integrated in a broader comparative framework, and its concordance or discordance with other craniognathic and postcranial evidence may be examined.

CONCLUSIONS

The past decade has witnessed increasing attempts to interpret the hominid fossil record within a framework of global and/or continental climatic, tectonic, and biotic changes (e.g., Vrba, 1985, 1988, 1996; Pickford, 1990; Tobias, 1991b; Turner and Wood, 1993b; Bromage and Schrenk, 1995). Such discussions, by necessity, must be based on sound empirical evidence of key evolutionary events involving the Hominidae. In this regard, a continuous fossil record is a must, and this is approximated only in eastern Africa. However, because this latter record is largely confined to the dental evidence, with much of it being fragmentary, care must be taken to realize both its limits and potentials. The morphological analysis presented above represents an attempt to unambiguously evaluate the eastern African quasicontinuous hominid record.

The early record

The earliest and extremely primitive hominid, *Ardipithecus ramidus* (White et al., 1994, 1995), is known to have existed as recently as 4.4 myr (WoldeGabriel et al., 1994, 1995). Subsequent to this, *A. anamensis*, a species more derived than *A. ramidus* and probably transitional to *A. afarensis*, has been reported from the 3.9–4.2 myr interval (Leakey et al., 1995). *A. afarensis* becomes widespread by circa 3.5 myr, as represented by the Ethiopian and Tanzanian fossil record (Leakey et al., 1976; Johanson and White, 1979; White et al., 1993). Kimbel et al. (1994) reported *A. afarensis* to have existed at Hadar at circa 2.95 myr, exhibiting no detectable morphological difference from the circa 3.4 myr condition.

The known first occurrence of *A. africanus* in southern Africa at Makapansgat is circa 2.8 myr by our biochronological evaluations

(Harris and White, 1979; White et al., 1984; Vrba, 1996). Foot bones recently reported from Sterkfontein Member 2 indicate hominid existence at that site prior to circa 2.5 myr (Clarke and Tobias, 1995), but these remain effectively undated (McKee, 1996; Tobias and Clarke, 1996). Although evidence is scant, the lack of hominids at the early Pliocene southern African site of Langebaanweg, recently documented to exhibit resemblances with the Aramis fauna (WoldeGabriel et al., 1994; unpublished observations), suggests an eastern to southern African dispersion of Hominidae to have taken place subsequent to the appearance of *A. afarensis* and prior to circa 2.8 myr bp.

Cladogenesis and evolution in East Africa

The results presented in this paper point out that by circa 2.9 myr, robust and nonrobust hominid lineages may have cooccurred for the first time in eastern Africa. By circa 2.7 myr there were certainly two contemporary hominid lineages, and subsequently robust *Australopithecus* specimens attributable to *A. aethiopicus* are known from Members C through F, spanning the circa 2.7 to 2.3 myr time range. These represent a morphotype suitable as ancestral to later *A. boisei*. They exhibit the derived robust *Australopithecus* morphology but lack the further specialized condition uniquely seen in *A. boisei* dentitions. It can also be said that *A. aethiopicus* shares with *A. robustus* the primitive robust conditions in the major features of the dentition, thus presenting itself as a potential ancestor of the South African *A. robustus*.

During the 2.7 to 2.3 myr time period, with the present small samples, no definitive time-transgressive trends were apparent in the East African robust lineage, a conclusion also reached by Wood et al. (1994) using a different data set. At circa 2.3 myr, a substantial phenetic transformation involving both teeth and mandible occurs (Suwa, 1988; Wood et al., 1994), but details of the highly derived *A. boisei* dental morphology emerge in a mosaic fashion across Member G times. This suggests that *A. aethiopicus* was indeed ancestral to *A. boisei* and hence reflects a

continuous robust *Australopithecus* lineage in eastern Africa (contra Skelton and McHenry, 1992).

Characterization of the East African nonrobust lineage is more difficult because of the polymorphic nature of detailed dental morphology, there being substantial overlap in ranges of variation among *A. afarensis*, *A. africanus*, and early *Homo*. Furthermore, interpretation of the record is confounded because of possible discordance of these dental details with more significant cranial features. The evidence put forward above, however, points to two likely possibilities that may be evaluated only by a less fragmentary hominid record. Thus, *A. africanus* may have been a wide-ranging species occurring in both southern and eastern Africa, occupying a phyletic position intermediate between *A. afarensis* and *Homo*; however, such a scheme would imply evolutionary parallelism and/or reversal in many craniodental features (e.g., White et al., 1981; Kimbel et al., 1984). Alternatively, the East African nonrobust lineage of the 2.9 to 2.5 myr time period may represent a direct transition from *A. afarensis* to early *Homo*, perhaps through a species yet to be identified.

By circa 2.4 myr, the postcanine dentition of the East African nonrobust lineage phenetically approximates the early *Homo* condition but lacks any specific affinities with *A. africanus*. These dentitions between 2.4 and 2.0 myr resemble the stated *Homo* "*rudolfensis*" condition (e.g., Wood, 1991b, 1993), while there is no evidence to falsify the null hypothesis of a single *Homo* lineage in eastern Africa during this time period. This leaves scenarios of a polyphyletic origin of *Homo*, such as given by Bromage and Schrenk (1995), to be without any empirical basis. Alternatively, if there was a single *Homo* lineage during the 2.4 to 2.0 myr time interval, then rapid evolution must have taken place at circa 1.9 myr, resulting in a restricted temporal overlap of at least two early *Homo* morphotypes.

This summary of Plio-Pleistocene hominid evolution, stemming from the analysis of the Omo dental collection, outlines a complex sequence of evolutionary events within the Hominidae of eastern Africa. At least four such events are suggested above: 1) a phy-

letic split occurring circa 2.95 to 2.7 myr resulting in *A. aethiopicus* and a nonrobust taxon most likely distinct from *A. afarensis*; 2) emergence of the *Homo* morphology at circa 2.5 to 2.4 myr; 3) phenetic specialization of the robust lineage at circa 2.3 to 2.2 myr producing the *A. boisei* condition; and 4) gracilization of the postcanine dentition in early *Homo* at circa 2.0 to 1.9 myr, possibly coinciding with a cladogenetic event. This cautions against simplified interpretations that are highly reliant on temporal correlations of, for example, hominid cladogenesis with singular climatic events.

South Africa

Relationships among the South and East African hominids are of prime importance in any evaluation of early hominid evolution. However, the unfortunate lack of a comparably continuous fossil record in southern Africa limits resolution of some key phylogenetic issues. Although many authorities regard the three robust *Australopithecus* species, *A. aethiopicus*, *A. boisei*, and *A. robustus*, to be monophyletic (e.g., Grine, 1988; Wood, 1991b), others have been impressed by similarities exhibited by the two South African taxa, *A. africanus* and *A. robustus* (e.g., Wolpoff, 1978; White et al., 1981; Rak, 1983). We take the position that this can ultimately be resolved in a stratophenetic manner only by the accumulation of time successive hominid samples in southern Africa.

If a robust *Australopithecus* monophyly was the case, then the East African record would have profound implications for interpretation of the South African hominids. Two major points emerge. Firstly, *A. africanus* could not be the ancestor of *A. robustus*, despite their similar geographical location and some morphological similarities. In this case, *A. africanus* would most likely represent an endemic species becoming extinct between circa 2.5 and 2.0 myr. Secondly, under robust *Australopithecus* monophyly, *A. robustus* would represent the end product of a phyletic split from the East African *A. aethiopicus*/*boisei* lineage, this taking place at circa 2.4 to 2.3 myr. While establishment of the southerly Transvaal distribution of *A. robustus* can only be estimated as greater

than 1.8 myr from the currently known fossil record, faunal associations with *Equus* and *Theropithecus oswaldi* (e.g., Turner and Wood, 1993a) suggest its possible presence in southern Africa anytime after circa 2.3 myr, perhaps linked with the spread of open environments.

Furthermore, a northerly origin of the Transvaal *A. robustus* populations would lead to a new interpretation of some long known peculiarities of the South African robust *Australopithecus* record. For some reason, Member 5 at Sterkfontein has yielded no remains of *A. robustus*, although recent reports suggest that this species may actually be represented in at least some of the Member 5 levels (Clarke, 1994). Despite broad temporal equivalence between Swartkrans Members 1 through 3 and Kromdraai B (Vrba, 1982; Delson, 1988; McKee, 1993; McKee et al., 1995), differences between the two *A. robustus* assemblages are well known in respect to deciduous molar and other craniodental morphologies (e.g., Howell, 1978; Grine, 1985). These aspects of the South African *A. robustus* record may simply be explained as a result of multiple incidences of fluctuation in geographical distribution of *A. robustus*. In this scenario, the geographical range of *A. robustus* during the circa 2.0 to 1.5 myr time period was centered to the north of the Transvaal region, with Swartkrans/Kromdraai representing the southerly areas experiencing successive episodes of local extinction and repopulation accompanied by genetic drift.

Earliest Homo

It can be seen that despite the currently available hominid record from the Shungura Formation, an almost complete gap in our knowledge exists regarding the transition of *A. afarensis* to *Homo* in eastern Africa, including the role that *A. africanus* may or may not have played in the emergence of the genus *Homo*. We confirm and emphasize here that this stems from an actual lack of hominid remains from lower Member C times, in step with the general paucity of collected fauna from lower to middle Member C horizons relative to the more abundant upper Member B and C records. With the

increasing complexity and confusion in our understanding of what exactly the South African species of *A. africanus* is (Kimbel and White, 1988; Kimbel and Rak, 1993; Clarke, 1988; Clarke and Tobias, 1995), it is all the more necessary to clearly document the non-robust lineage of eastern Africa of the 3 to 2.5 myr time period. In particular, the results of the present study indicate that specifically the lower/middle Member C time horizons, spanning the 2.9 to 2.7 myr time interval, should be the target for focused field research to unravel this critical segment of the hominid phylogenetic tree.

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APPENDIX

Approximately half of the Omo dental sample of the present study is illustrated here. The remaining specimens are figured in Howell (1969a), Coppens (1970, 1971, 1973a,b) or Howell and Coppens (1976). All occlusal views are with mesial toward the top. All isolated teeth are approximately twice natural size. The two partial mandibles are approximately natural size. Note that in these photographs orientation was not controlled for measurement.

1: OMO123-5495, aff. *Homo* sp., right P3, mesial and occlusal views. 2: OMO33-5496, aff. *Homo* sp., left P3, mesial and occlusal views. 3: L465-111, *A. aethiopicus*, left P3. 4: L398-120, *A. aethiopicus*, right P3. 5: OMO177-4525, aff. *Homo* sp., right P3. 6: L628-4, *A. aff. aethiopicus/boisei*, left P4. 7: L338x-40, *A. aethiopicus*, left P4. 8: L51-79,

A. aethiopicus, right P4. 9: L51-80, nonrobust *Australopithecus/Homo* indet., right P4. 10: L628-9, *A. aff. boisei*, left M1. 11: L157-35, *A. aethiopicus*, left M2. 12: L62-17, *A. aethiopicus*, right M2. 13: OMO47-46, *A. aff. boisei*, right M2. 14: OMO33-6172, *A. aethiopicus*, right M3. 15: L398-630, *A. aethiopicus*, right M3. 16: L296-1, *A. aethiopicus*, right M3. 17: L338x-39, *A. aethiopicus*, left M3. 18: L628-3, *A. aff. boisei*, left M3. 19: L628-2, *A. aff. boisei*, right M3. 20: OMO212-1950, nonrobust *Australopithecus/Homo* in-

det., left M1. 21: L824-5, nonrobust *Australopithecus/Homo* indet., left M1. 22: OMO195-1630, aff. *Homo* sp., right M1. 23: L7-279, aff. *Homo* sp., left M2. 24: L628-10, aff. *Homo* sp., left M2. 25: L795-1, taxon indeterminate, right M2. 26: L1-398, nonrobust *Australopithecus/Homo* indet., right M3. 27: L1-294, nonrobust *Australopithecus/Homo* indet., right M3. 28: L427-7, *A. aff. boisei*, right mandibular corpus with P3 to M2. 29: L55-33, *A. aethiopicus*, left mandibular fragment with I1 to P4.

